

PRESIDENTIAL ADDRESS

The Ordovician Stromatoporoids

B. D. WEBBY

Department of Geology & Geophysics, University of Sydney

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Synopsis

Stromatoporoids are sessile, dominantly Early-Middle Palaeozoic, frame-building, calcareous fossils, probably nearest to present-day sclerosponges or hydrozoans. The Ordovician representatives, which formed important constituents of the earliest coral-stromatoporoid-algal patch reef and carbonate bank communities, include members of three markedly different families — the Labechiidae, the Clathrodictyidae and the Cliefdenellidae. The labechiids are the most diverse and abundant Ordovician group with some nineteen genera, and a maximum development in the Middle-Late Ordovician. The clathrodictyids are a predominantly Silurian family, but three genera had already appeared in the preceding Ordovician. The cliefdenellids are restricted to one, exclusively Ordovician, genus. A systematic review of all the constituent Ordovician genera is presented.

The distribution of the genera is depicted in terms of the known Ordovician stratigraphical ranges and geographical spread. The labechiids exhibit a strikingly rapid period of diversification in the Middle Ordovician (in North American stratigraphical terminology, between Chazy and 'Blackriver' times). Most genera appear to have dispersed fairly rapidly along the band-like Ordovician 'equatorial' belt, but a few like *Pachystylostroma* and *Aulacera* seem to have migrated much more slowly, having taken until late in the Ordovician to achieve a circum-equatorial distribution. The clathrodictyids and cliefdenellids made their first appearances in the Australian region in the late Middle Ordovician (North American 'Trenton'). *Clathrodictyon* and *Ecclimadictyon* also migrated very slowly, taking until the end of the Ordovician to attain a circum-equatorial dispersal. While the clathrodictyids may have evolved from a simple 'vesicular' Middle Ordovician labechiid, it is more difficult to derive the complex morphology of *Cliefdenella* from such an ancestor. *Cliefdenella* is only recorded from Australia and Siberia.

The supposed Cambrian 'stromatoporoids' cannot be positively confirmed as the ancestral stocks to later stromatoporoids. They have a temporally and geographically restricted occurrence in the Early Cambrian of the Altai Sayan mountain region of Siberia, have archaeocyathan associations and morphological resemblances to some members of the class Irregulares, and they are separated by a period of 110 million years from indubitable Middle Ordovician and later stromatoporoids. An earlier ancestry would help to explain the sharp morphological differences between individual families and to resolve the problem of the derivation of *Cliefdenella*, but the origins may have been in non-skeletonized stocks rather than in the supposed Cambrian 'stromatoporoids'. The first Ordovician appearance of each family seems more likely to reflect the beginnings of skeletonization in the particular group rather than to depict the initial radiation of a new lineage. The review concludes with an account of the adaptive radiation of skeletonized Middle-Late Ordovician labechiid genera, and an outline of the alternatives for deriving the clathrodictyids and the cliefdenellids.

INTRODUCTION

The year 1978 marked the centenary of the introduction by Nicholson & Murie of the term Stromatoporoidea. Members of this problematical group of fossil organisms have calcareous skeletons of hemispherical, laminar, encrusting, cylindrical and ramose growth form, and are composed internally of a meshwork of plate-like elements (cysts or laminae) and intersecting, vertical, rod-like pillars, or less

commonly, an amalgamate network. Nicholson & Murie (1878) reviewed the structure and affinities of stromatoporoids — published incidentally in the journal of our kindred society, the Linnean Society of London — arguing against their affinity with marine plants ('Nullipores'), Foraminifera, hexactinellid sponges, Bryozoa and corals. They noted the close resemblances to hydrozoans and to calcareous sponges, favouring a grouping with the sponges. Later, Nicholson (1886a) revised this view in favour of interpreting stromatoporoids as hydrozoans rather than sponges, having become convinced of the existence in various typical stromatoporoids of 'tubes' or 'cells' which may have served to house living zooids as in a coelenterate colony.

Both Nicholson & Murie's earlier interpretation and Nicholson's later grouping have their modern adherents. Stearn (1975) has summarized the divergence of opinion as between 'those who maintain that they are hydrozoans whose closest living relative is *Hydractinia* and those who believe that their closest living relatives lie in the Phylum Porifera. In favouring the assignment of them to a separate subphylum of the Porifera (the Stromatoporata), Stearn (1972; 1975) noted the morphological similarities, especially the presence of astrorhizae (possibly representing the excurrent canal system as in a sponge), and the principal difference in lacking siliceous spicules. He interpreted the stromatoporoids like modern sclerosponges as secreting a skeleton of fibrous aragonite and living as individual (non-colonial) filter feeders.

On the other hand, Birkhead (1967), Flügel & Flügel-Kahler (1968), Sleumer (1969), Mori (1969; 1970), Bogoyavlenskaya (1969), Kaźmierczak (1971) and Bolshakova (1973), among modern specialists of the group, prefer to view them as having an affinity with hydrozoans. Kaźmierczak (1976), though, in the latest expression of his views, radically departs from his earlier interpretation, and now proposes that stromatoporoids be removed from the animal kingdom, and included with stromatolites in the Cyanophyta (blue-green algae). Thus the precise affinities and systematic relationships of stromatoporoids are now little closer to being settled than they were in Nicholson's day, despite the enormous increase in knowledge of the group, including the especially important contributions on microstructure (Stearn 1966; St. Jean 1967) and soft tissue reconstructions based on analogies with living sclerosponges (Stearn 1975).

The majority of past and present-day specialists have viewed the Stromatoporoidea as being a reasonably homogeneous group. However, a small band of European workers, notably Heinrich (1914), Tripp (1929), Kühn (1927; 1939) and Alloiteau (1952), have considered them to be heterogeneous, with representatives of the family Labechiidae taken to be a separate subdivision not allied to stromatoporoids proper. These workers maintained that the coenosteum (or skeleton) of members of the order Stromatoporoidea in exhibiting a meshwork of open, gallery-like passages and a ramifying, tube-like astrorhizal system, differed fundamentally from labechiids which typically have a closed vesicular form and lack astrorhizae. The labechiids were therefore assigned to a separate order. The majority of present-day specialists of the group (Yavorsky 1962; Nestor 1964; 1966a; 1966b; Stearn 1966; Flügel & Flügel-Kahler 1968; Webby 1969; Bogoyavlenskaya 1969; Mori 1969; 1970; Bolshakova 1973; Khalfina & Yavorsky 1973; Khromych 1974a; and Kapp & Stearn 1975), however, include the labechiids in the Stromatoporoidea. As Nestor (1966a) has said, 'the differences between the vesicular and other stromatoporoids are by no means so sharp and fundamental as to justify assigning them to different orders'.

Many previous workers have alluded to the difficulties of interpreting — more specifically identifying — stromatoporoids because of their susceptibility to alteration both by the processes of diagenesis and recrystallization. Stearn's (1972; 1975) explanation that stromatoporoids initially secreted a more unstable aragonite skeleton

recalls Nicholson's (1886a, p. 35) original statement. He wrote: 'There is, in fact, considerable reason for concluding that the skeleton was originally composed of arragonite, and that in almost all, or perhaps all, specimens which have not been silicified, the arragonite has become more or less extensively replaced by calcite'. Other calcareous fossil groups such as brachiopods, bryozoans and some corals (notably heliolitids) usually exhibit better preservation than the associated stromatoporoids (Kapp & Stearn 1975).

Not only are there problems of interpreting the effects of secondary alteration of the original structure, but there are difficulties in recognizing the limits of the original variability within many fossil species. For instance, within a single coenosteum exhibiting alternate banding of two distinctive morphologies, one may be inferred to be more completely calcified than the other (see further discussion p. 87, and Yavorsky, 1961, pl. 19, figs 1-6; pl. 20, figs 1-2). The coenosteum may have been better calcified at certain periods of growth than at others (Kapp & Stearn 1975).

The first, indubitable representatives of the Stromatoporoidea appeared in the Middle Ordovician (Chazy) of eastern North America (Galloway 1957; Kapp & Stearn 1975), and the group rapidly attained a wide distribution through Europe, Asia, North America and Australia. The position of the problematical, Early Cambrian stromatoporoids from the Altai Sayan fold belt of south west Siberia (Khalfina & Yavorsky 1967) remains in doubt (see later discussion p. 112). The Middle-Late Ordovician stromatoporoids accumulated in carbonates mainly in isolated occurrences, small clusters or bank-type deposits (biostromes). In a few places they are also reported as constituting a conspicuous component of patch reefs (bioherms), for instance, in the early Middle Ordovician Chazy Group of Vermont (Kapp 1975), in the late Middle Ordovician Mjøsa Limestone of Norway (Skjeseth 1963), and in the Late Ordovician (Richmond) of Anticosti Island (Bolton 1972; Copper, 1974). The Ordovician stromatoporoids merit close attention for a fuller understanding of the structure and development of the early members of the group.

In an attempt to maintain uniformity of usage throughout this review, I have followed North American practice of regarding the Whiterock, Chazy, 'Blackriver' and 'Trenton' as Middle Ordovician, and the Eden, Maysville and Richmond as Late Ordovician (see Fig. 8). Specimens illustrated in Figs 1-7 are from the following repositories: palaeontology collection of Sydney University (SUP), geology collection of the University of Tasmania (UTGD), Paleontologisk Museum, Oslo (PMO), and the Sedgwick Museum, Cambridge (SM).

SYSTEMATIC REVIEW

In general Ordovician stromatoporoid faunas tend to be less well preserved, and less diverse and abundant than their Middle Palaeozoic counterparts. Representatives of only three families have been confirmed as occurring in Ordovician strata (Webby 1969; Webby & Morris 1976) — the Labechiidae Nicholson 1879 being the largest and most varied family with its maximum development in the Middle-Late Ordovician, the Clathrodictyidae Kühn 1939, a relatively inconspicuous component of the Middle-Late Ordovician fauna, and the Cliefdenellidae Webby 1969, limited to a single, exclusively Ordovician genus.

(a) *Family Labechiidae*

The conception of the family adopted herein is similar to that given by Galloway (1957), Yavorsky (1962) and Stearn (1966) — it appears to be a natural grouping, and is not easily amenable to subdivision. The group could be enlarged to superfamily

rank but is still not easily subdivisible. It constitutes the elements of 'Gruppe 1' of Flügel & Flügel-Kahler (1968). The family includes a wide range of forms characterized by imperforate, compact tissue, cyst-like to laminar plates, sometimes exhibiting denticles, sometimes pillars (occasionally both), and with very rare obscure occurrences of astrorhizae (Yabe & Sugiyama 1930; Nestor 1966b; 1976; Mori 1970).

Some workers (Kühn 1927; 1939; Lecompte 1956) have separated the cylindrical to branching forms from the rest of the group, placing them in the family Aulaceridae Kühn 1927. However others, such as Bogoyavlenskaya (1969; 1971) and Khalfina & Yavorsky (1973), regard the shape of the coenosteum as a feature of generic not family rank.

Bogoyavlenskaya (1969; 1974) has raised labechiids to the level of an order, and Khalfina & Yavorsky (1973) and Nestor (1974; 1976) to that of a superfamily. New family subdivisions have been added — Stromatoceriidae Bogoyavlenskaya 1969, Plumataliniidae Bogoyavlenskaya 1969, Rosenellidae Yavorsky in Khalfina & Yavorsky 1973, and Platiferostromatidae Khalfina & Yavorsky 1973 — but all seem to be unnatural divisions and should be rejected. Also, Khalfina & Yavorsky assign without comment the family Stromatoceriidae (genus *Stromatocerium* Hall) to stromatoporaceans rather than labechiaceans.

The erection of the family Lophiostromatidae Nestor 1966 (superfamily Lophiostromatacea Nestor 1974) seems to be another unnecessary subdivision of the labechiid group, introduced in order to accommodate those elements with more massive tissue (the genera *Lophiostroma* Nicholson 1891 and *Dermatostroma* Parks 1910).

Nestor (1974) proposed a four-fold subdivision of the superfamily Labechiacea — families Labechiidae, Stromatoceriidae, Aulaceridae and Plumataliniidae. In a subsequent paper, Nestor (1976) offered a different four-fold subdivision adding the Rosenellidae and subtracting the Stromatoceriidae. He radically changed the generic composition of the various families from his earlier subdivision. For example, the Aulaceridae which formerly included only the cylindrical forms (such as *Aulacera*, *Sinodictyon* and *Cryptophragmus*) was modified to include *Cystistroma* Etheridge and *Stromatocerium* Hall, and to exclude *Cryptophragmus* and *Sinodictyon* — to group together the cystose forms with 'hollow' pillars irrespective of their growth form. The 'hollow' pillars of *Stromatocerium*, as Kapp & Stearn (1975) have remarked, may form by diagenetic processes from solid ones, and therefore may have little or no taxonomic significance.

Khromych (1974a; 1974b) has given as the basis for subdividing the labechiids, the presence or absence of continuous pillars with an inverted cone-like structure, but has actually provided a most arbitrary and artificial subdivision of the group. Clathrodictyids are associated with forms like *Stromatocerium* (Stromatoceriidae) and *Cystostroma* (Cystostromatidae Khromych 1974a) in the same superfamily (Cystostromacea), and representatives of the family Labechiidae (restricted) are placed with members of the family Actinostromatidae in the superfamily Labechiacea. *Stromatocerium* which has close ties to *Labechia* and *Labechiella* (differing chiefly in having angular to blade-like instead of round pillars) is thus grouped in a separate superfamily from *Labechia* and *Labechiella* — placed in the superfamily Cystostromacea (and associated with *Clathrodictyon*). This is as extreme and as unacceptable as Khalfina & Yavorsky's (1973) grouping of *Stromatocerium* in the superfamily Stromatoporacea.

Kaźmierczak (1971) has employed a two-fold morphological grouping with subdivisions (lineages) based on inferred evolutionary trends. Morphological group

A, lineages I-IV, contain many common labechiid genera, but the individual lineage subdivisions fall well short of acceptable natural groupings. The worst example is the association of the morphologically distinctive, non-labechiid *Cliefdenella* Webby with the labechiid *Forolinia* Nestor in lineage IV.

The Ordovician representatives of the family Labechiidae exhibit a wide variety of growth form. As Parks (1910) noted, they range from 'delicate incrustations of *Dermatostroma papillatum*' to giant cylindrical columns of *Aulacera* like those found on Anticosti Island up to 5 metres long and 350 mm in diameter (Galloway & St. Jean 1961, p. 26). They occur, however, more commonly in hemispherical to sheet-like masses — for example, the hemispherical masses of *Cystistroma donnellii* Etheridge from the Cliefden Caves Limestone of New South Wales attain dimensions of 280 mm across and 200 mm in height (Webby 1969), and *Labechia huronensis* (Billings) from the Late Ordovician of Ontario, Indiana and Ohio has a size of up to 270 mm across and 120 mm in height (Galloway & St. Jean 1961). Some masses of *Cystostroma* such as *C. fritzae* Galloway & St. Jean from the Late Ordovician of Ontario attain larger dimensions — 600 mm across and 250 mm in height. Kapp (1974; 1975) reported the occurrence of a still larger conical to columnar coenosteum of *Pseudostylodictyon lamottense* (Seely), more than 1 metre in width and height from the Chazy Group of eastern North America.

(i) *Cystostroma* Galloway & St. Jean in Galloway 1957 — Kapp & Stearn (1975) questioned the validity of the genus *Cystostroma* based on the type species *C. vermontense* Galloway & St. Jean from the Crown Point Formation (Chazyan) on Isle La Motte. In a survey of some 400 specimens from the type area, the morphology of *C. vermontense* was only found at the bases of coenostea of *Labechia prima* Kapp & Stearn and some other species. However in the type material re-examined by Kapp & Stearn only the vesicular *Cystostroma* cyst-type structure is preserved.

The problem of intergrowths of two distinct morphologies in one coenosteum is highlighted by another example from the Late Ordovician of the Kolyma Basin, north-eastern U.S.S.R. Identified by Yavorsky (1961) as an intergrowth of *Labechia mirabilis* Yavorsky and *Cystostroma rarum* Yavorsky this labechiid exhibits alternating phases of growth with cysts only, giving a *Cystostroma* morphology, and with both cysts and pillars producing a *Labechia*-type structure. In another example of an undescribed species from the lower part of the Gordon Limestone Subgroup near Mole Creek, Tasmania, the bands of cysts alternate with sediment layers (less commonly diagenetic silt). Some individual coenostea (Fig. 2E-F) show little trace of pillars, while others exhibit, in varying stages of preservation, solid pillars or 'wall-less rods' (Kapp & Stearn 1975). It is therefore assigned to *Labechia*.

Many of the designated species of *Cystostroma* exhibit denticles, and some even show impersistent pillars, of the type formed by superposition of denticles through more than one cyst. The problem is where to draw the line between forms with denticles only and forms with impersistent pillars. The type species *C. vermontense* (based on the type material) and *C. cliefdenense* Webby seem to lack all traces of pillars, whereas Nestor's (1964) *C. estoniense* is recorded as having rare, short, 'hollow' pillars, and *C. concinnum* Ivanov in Ivanov & Myagkova from the Late Ordovician of the Urals (Bogoyavlenskaya 1973) also has occasional slender, tubule-like pillars. Nestor (1976), who includes forms with impersistent pillars in his conception of the genus, has listed some thirteen species from the Middle-Late Ordovician.

Little has been written on the ontogeny of species as a basis for determining stromatoporoid ancestry and phylogeny (see Galloway 1957). The basal row of cysts or laminae of the coenosteum (and the basal rows of successive latilaminae) may provide

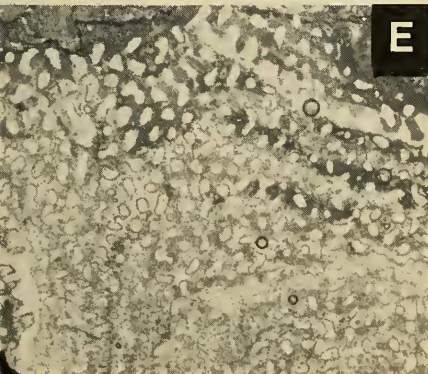
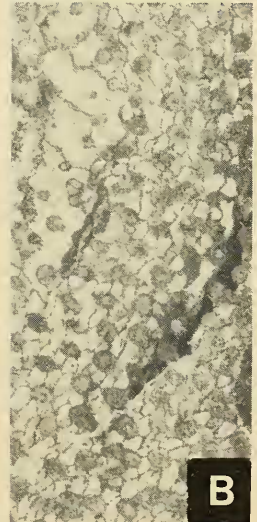
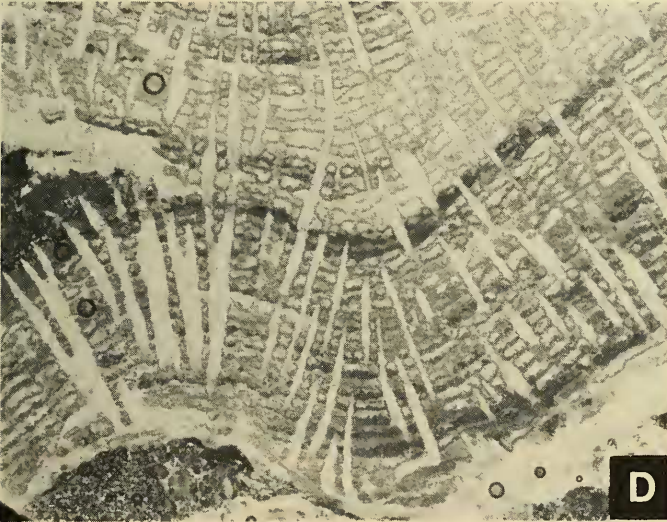
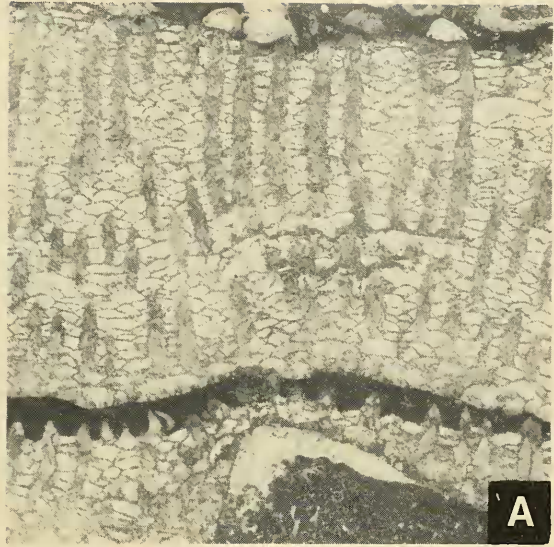
some clues to the early developmental stages of a particular line. In this context, Kapp & Stearn's (1975) observation that the structure of *C. vermontense* is only preserved in the bases of coenostea of *Labechia prima* and other species may be significant in supporting arguments that *Cystostroma* is the 'ancestral' stock. The base of the coenosteum of *Labechia* cf. *L. pustulosa* (Safford) — see Kapp & Stearn (1975, pl. 4, fig. 3) — and the base of a latilamina of *L. aldonesis* Webby (1977, pl. 1d) similarly exhibit a *Cystostroma*-type structure.

(ii) *Pseudostylodictyon* Ozaki 1938 — The type species, *P. poshanense* Ozaki 1938, following the definitions of cysts and laminae given by Kapp & Stearn (1975, p. 167), exhibits both cysts and laminae, but in some parts of the coenosteum it is difficult to distinguish between them. The laminae seemingly form parallel to the growth surface of the coenosteum, and represent successive depositional floors. The cysts, both large and small, fill interspaces between successive depositional floors in two main areas, on the slopes of the mamelons and in the troughs between the mamelons. Denticles may be present or absent. The problem of whether the laminae are original, laterally continuous, plate-like structures, or formed secondarily by the destruction of inclined-vertical side walls of long-low cysts in certain rows during diagenesis or recrystallization, is unresolved. At least in *P. inequale* Webby (1969, pl. 119, figs 1-3) its laterally continuous concentric plates appear to represent original primary laminae (Fig. 3F).

Kapp & Stearn (1975) have expressed inconsistent statements bearing on the early stages of stromatoporoid evolution. On the one hand (p. 169) they claim that *Labechia eatoni* (Seely) with its rows of similar-sized long-low cysts arose from *Pseudostylodictyon lamottense* (Seely) with its pattern of predominant laminae, and on the other (p. 167), they maintain that 'primitive' species have large, strongly convex cysts of variable size and shape, while more advanced forms have smaller, more uniform long-low cysts, implying a more probable derivation of the Chazy *Labechia* from a vesicular *Cystostroma*-like ancestor. If *Pseudostylodictyon* is indeed ancestral to *Labechia*, why do not the bases of coenostea of *Labechia* exhibit a 'laminar' *Pseudostylodictyon* structure?

Plumatalinia Nestor 1960 has been distinguished from *Pseudostylodictyon* by having a fine subreticulate tissue in the mamelon columns (Nestor 1964). However, it remains uncertain as to whether this tissue is of primary or secondary origin. If the latter, then the original vesicular plates of the mamelon columns have broken down into a secondary subreticulate tissue; and hence the genus should be regarded as a synonym of *Pseudostylodictyon*. In an opposed view, Bogoyavlenskaya (1969) has argued that *Plumatalinia*, because of its morphology of vesicular plates resembling laminae, and reticulate column network, could well be the ancestor of 'laminar' stromatoporoids, for instance the clathrodictyids. She introduced the family Plumataliniidae to accommodate this genus.

Fig. 1. A-B, *Labechia conferta* (Lonsdale 1839), $\times 5$, SUP 285 from the Silurian of Dudley, England. A, vertical section showing solid pillars protruding upward into the sediment. B, tangential section. C-F, *Stromatocerium* sp. nov., $\times 5$, from the lower part of the Gordon Limestone Subgroup (Middle Ordovician) of Tasmania. C, vertical section of UTGD 94642 from the Cashions Creek Limestone of the Florentine Valley showing peripheral part of latilaminar coenosteum. D, vertical section of UTGD 94639 exhibiting diagenetically altered, sparry calcite-filled pillars. E, tangential section of UTGD 94640. F, vertical section of UTGD 94641 showing sparry calcite-filled (replaced) pillars protruding into the overlying sediment. D-F, from the lower part of section on the south-west side of Sassafras Creek in the Mole Creek area.



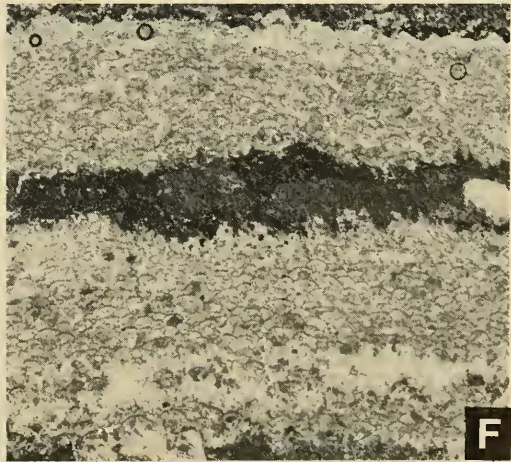
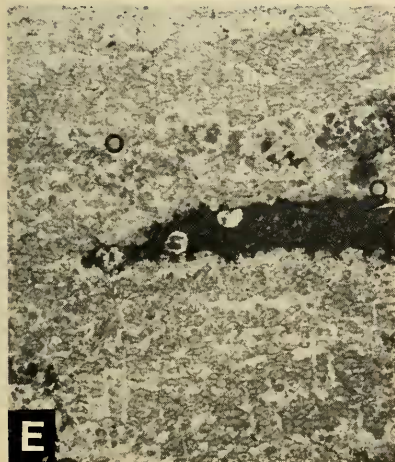
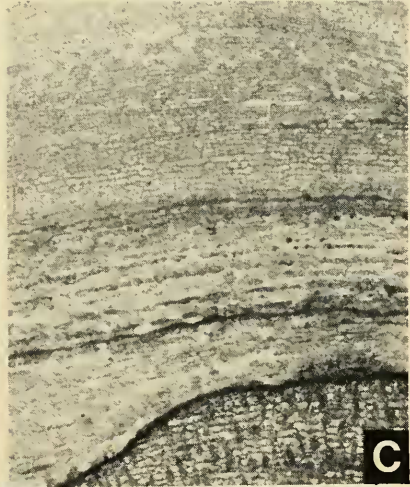
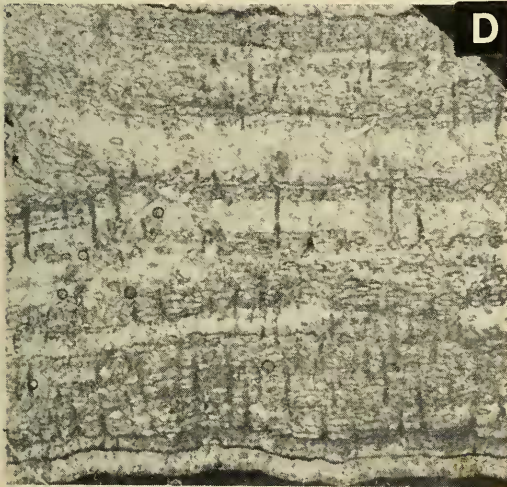
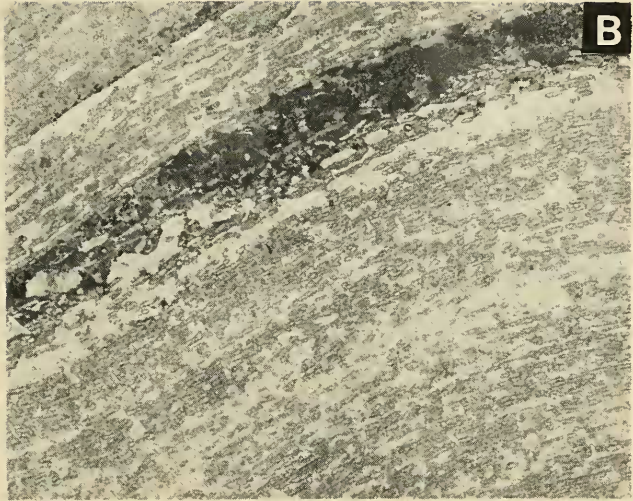
(iii) *Labechia* Milne-Edwards & Haime 1851 — The internal structure of *Labechia* based on the type species *L. conferta* (Lonsdale) from the Middle Silurian of England has been fully investigated by Nicholson & Murie (1878) and Nicholson (1879), and shown to be composed of a large number of stout, vertically aligned pillars with a series of lenticular, upwardly convex vesicles filling the interspaces (Fig. 1A-B). The pillars, Nicholson (1879; 1886a) noted, protrude onto the upper surface of the coenosteum as solid tubercles (papillae), but may show axial canals elsewhere. Because of the irregular arrangement of the vesicles (Nicholson 1886a), the coenosteum exhibits little tendency to split concentrically as in typical stromatoporoids with 'concentric laminae'. Lecompte (1956), Galloway (1957), Galloway & St. Jean (1961), Yavorsky (1962), Nestor (1966b) and Mori (1970) offered a similar generic conception to that given by Nicholson, emphasizing the long, stout, round pillars, vesicular cyst plates and compact microstructure. The pillars may have an upwardly-directed cone-in-cone appearance, zigzag-shaped outer edges and axial canals as seen in vertical section, and concentric banding with lighter, apparently hollow centres (intersected axial canals) as seen in tangential section (Stearn 1966; Nestor 1966b). In fact the axial canals are not strictly hollow but have an infilling of sparry calcite.

Only a few Ordovician species, like *Labechia huronensis* from the Late Ordovician of Canada (Galloway & St. Jean 1961), bear close morphological similarity to the type species, *L. conferta*. Other forms, with only a patchy development of pillars, and with more consistency in the regularity of horizontal cyst rows than in the continuity of vertical pillars, have been included in the genus; see, for example, *Labechia eatoni* (Seely 1904), *L. prima*, Kapp & Stearn 1975 and *L. aldonensis* Webby 1977. In the group including these species (*L. prima* group), the coenosteum has an overall appearance of more conspicuous horizontal elements than vertical (Figs 2D; 3C-D), in contrast to those closely allied to the type species (*L. conferta* group) with the continuity of strong, vertical pillars as the dominating feature of their coenostea (Fig. 1A-B). The *L. prima* group is well developed in the Middle-Late Ordovician, from the middle Chazyan onwards, and probably represents an early stage in the evolutionary development of *Labechia*.

Stearn (1966) noted that the cysts of virtually all labechiids appear to be without pores except in the genus *Forolinia* Nestor 1964. He suggested that if the supposed foramina in the cysts of this genus are leached or recrystallized pillars then the genus would be difficult to distinguish from *Labechia*. Kapp & Stearn (1974) have added that if the 'canals' of Nestor (1964) are interpreted as altered pillars, then *Forolinia* should be regarded as a synonym of *Labechia*.

(iv) *Labechiella* Yabe & Sugiyama 1930, *Labechiellata* Sugiyama 1940 and *Tuvaechia* Bogoyavlenskaya 1971 — Yabe & Sugiyama (1930) introduced *Labechiella* as a subgenus of *Labechia* but misinterpreted the flattened cyst plates

Fig. 2. A-B, *Stratodictyon* sp. nov., from the lower part of the Gordon Limestone Subgroup on south-west side of Sassafras Creek, Mole Creek area, Tasmania. A, vertical section of UTGD 94643 showing pillars. Note coenosteum is cut by large calcite vein. B, vertical section of UTGD 94644 with banding seemingly partially due to replacement of rows of long-low cysts. Sparry calcite fills the diagenetically altered areas — the scattered former pillars (now 'wallace rods') and the rows of cysts (in part resembling laminae). C, association of holotype of *Stratodictyon ozakii* Webby 1969 on *Labechiella regularis* (Yabe & Sugiyama 1930); SUP 26252, $\times 5$, from lower part of Cliefden Caves Limestone at Licking Hole Creek, central western New South Wales. D, vertical section of *Labechia* of the *L. prima* type from the lower part of the Gordon Limestone Subgroup, south-west side of Sassafras Creek, Mole Creek area, Tasmania; UTGD 94645, $\times 5$. E-F, *Labechia* sp. A, $\times 5$, latilaminar coenostea from lower part of the Gordon Limestone Subgroup in cliff section on north side of Sassafras Creek, Mole Creek area. E, vertical section of UTGD 94646 showing a few traces of former pillars — now 'wallace rods'. F, vertical section of UTGD 94647, which in contrast lacks all traces of pillars.



(laminae) of the type species *Labechia serotina* Nicholson from the Middle Devonian of England as rod-like horizontal elements. The rounded pillars of *L. serotina*, as seen in tangential section, characteristically unite into chain-like groups (Galloway, 1957).

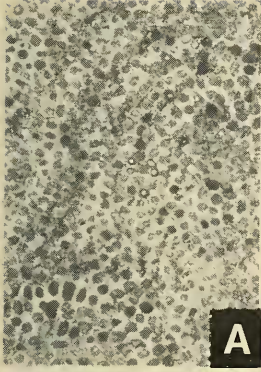
Following the introduction of *Labechiella* Sugiyama (type species *Labechiella regularis* Sugiyama 1939 from the Silurian of Japan) in 1939, Sugiyama appears to have realized his error of using a preoccupied name, for in the errata column of his 1940 paper he substituted the new name *Labechiellata* Sugiyama 1940. In his next paper Sugiyama (1941) again referred to *Labechiellata*. The type species of *Labechiella* Yabe & Sugiyama 1930 and the type species of *Labechiellata* Sugiyama 1940 are closely similar except for the spacing of pillars; in *Labechiella serotina* they are close spaced and tend to form chain-like links as seen in tangential section, while in *Labechiellata regularis*, the vertical rod-like pillars are widely spaced. Galloway (1957) has argued that Sugiyama (1939; 1940) incorrectly claimed credit for erecting the genus *Labechiella* based on *L. regularis* Sugiyama, and that the introduction of the name *Labechiellata* Sugiyama 1941 (*sic*) could only be explained by a memory lapse on Sugiyama's part. However, as outlined above, Sugiyama's actions seem to be more readily explained in terms of his recognition of the error and substitution of the new name *Labechiellata*.

Bogoyavlenskaya (1971) has added the new genus *Tuvaechia* (type species *Labechia regularis* Yabe & Sugiyama 1930, *non Labechiella regularis* Sugiyama 1939). Nestor (1976) in discussing the relationships between *Tuvaechia* and *Labechia* pointed out the lack of clear-cut distinctions between the shape of the vesicles, the spacing of the pillars and the stratigraphical distribution of the two forms. The differentiation between *Tuvaechia* and *Labechiella* is even more difficult. *Tuvaechia*, like *Labechiellata* is distinguished from *Labechiella* only by the wider spacing of the pillars. Like *Labechiellata* it should be regarded as a junior synonym of *Labechiella*. *Labechiella regularis* Sugiyama 1939 thus becomes a subjective junior synonym of *Labechiella regularis* (Yabe & Sugiyama 1930) and must be renamed; I propose *Labechiella sugiyamai* sp. nov.

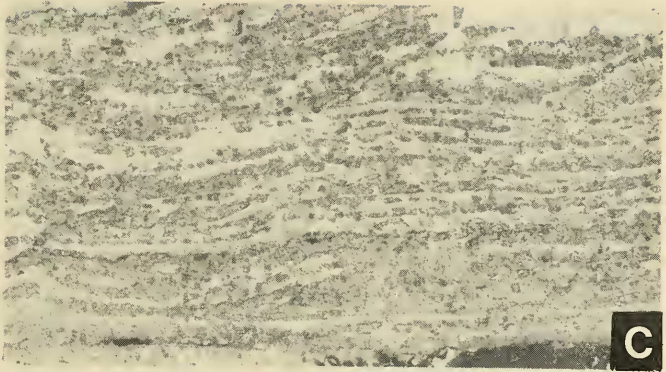
Whether *Labechiella* (Fig. 3A-B) was derived from a *Labechia* by flattening of cyst plates to form laminae or from a *Pseudostylodictyon* by superposition of the denticles to form strong continuous pillars remains in doubt. Galloway (1957, p. 393) claimed a derivation of *Labechiella* from *Labechia*. The developmental trend proposed by Bogoyavlenskaya (1971) involving evolution first of *Labechia* from *Tuvaechia* (= *Labechiella*), and second of *Labechiella* from a *Labechia*, does not seem to accord with present known facts about morphological relationships and stratigraphic distribution (see Nestor 1976, p. 37).

(v) *Stratodictyon* Webby 1969 — The conception of *Stratodictyon* is here

Fig. 3. A-B, *Labechiella regularis* (Yabe & Sugiyama 1930) from the lower part of the Cliefden Caves Limestone, central western New South Wales; $\times 5$. A, tangential section of SUP 26240 from west of Boonderoo shearing shed. B, vertical section of SUP 26236 from Licking Hole Creek. Note well developed primary laminae. C, *Labechia* sp. B; vertical section of PMO 97117 from Mjøsa Limestone south of Bergvika, Norway, showing diagenetically produced, 'secondary' laminae; $\times 5$. D, *Labechia aldonensis* Webby 1977; vertical section of paratype SM.A97446 from Stinchar Limestone near Girvan, Scotland, exhibiting incipient, diagenetically formed, secondary laminae; $\times 5$. E, *Cystistroma donnelli* Etheridge 1895; vertical section of assumed topotype SUP 28246 from lower part of Cliefden Caves Limestone at Fossil Hill, central western New South Wales, $\times 4$. Note small denticles on upper surfaces of cysts. F, *Pseudostylodictyon inequale* Webby 1969; vertical section of paratype SUP 29134 from Clearview Limestone Member of Ballingoolle Limestone (Bowen Park Group), Malachi's Hill, central western New South Wales; $\times 10$. Note the presence of both cysts and primary laminae.



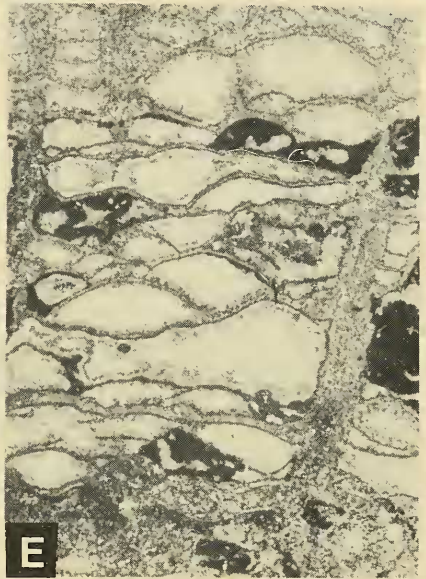
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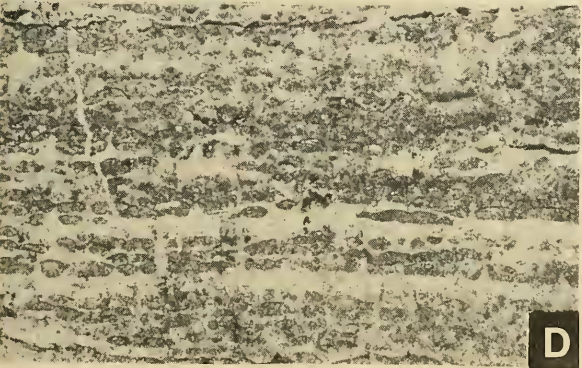
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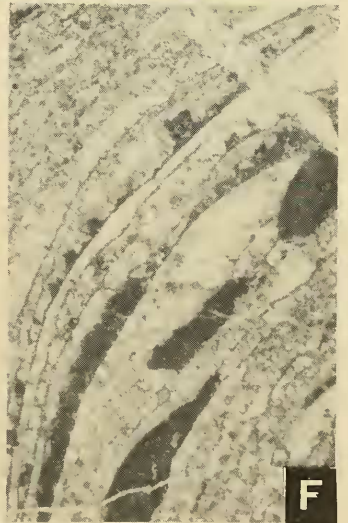
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D



F

restricted to include only those fine textured, latilaminar forms with horizontal elements composed of regular, close-spaced rows of long-low cysts resembling incipient laminae, vertical elements consisting of denticles and small, discontinuous pillars occupying some areas of the coenosteum but not others, and seemingly lacking astrorhizae (cf. Webby 1969). The notion of Galloway (1957, p. 364) and Kapp & Stearn (1975, p. 167) that 'primitive species have cysts which are large, strongly convex, and variable in shape and size' and that more advanced forms have smaller cysts with a higher length/height ratio and more uniform character may be used to imply that *Stratodictyon* — the type species *S. ozakii* Webby (Fig. 2C), and *S. columnare* Webby, from the Cliefden Caves Limestone of New South Wales, an undescribed species from the Gordon Subgroup of Tasmania (Fig. 2A-B), and *S. valcourensis* (Kapp & Stearn) from the late Chazy of eastern North America — is a more advanced form than the representatives of the *Labechia prima* group. In *L. prima* Kapp & Stearn, *L. eatoni* (Seely) and *L. aldonensis* Webby, the cysts are less regular in size and shape, and they are less conspicuously aligned in regular rows appearing as incipient laminae.

(vi) *Rosenella* Nicholson 1886a — This morphologically simple genus is typified by its exhibiting variably sized, usually large, cysts, with or without denticles (Nicholson 1886a; 1886b; Galloway 1957; Galloway & St. Jean 1961). *Rosenella* (Fig. 5D) may be distinguished from *Cystostroma* by having relatively much larger and more variably sized cysts, and from *Pseudostylodictyon* by lacking clearly defined laminae.

(vii) *Pachystylodictyon* Nestor 1964 — As pointed out elsewhere (Webby 1979), the selection of the type species of *Pachystylodictyon*, *P. ungeri* (Rosen) from the early Silurian of Estonia, seems to have been an unfortunate choice, for it lacks indubitable pillars (see Nestor 1962; 1964). Indeed, at the generic level, it is indistinguishable from a *Pseudostylodictyon*, and even bears a resemblance to the type species of that genus, *Pseudostylodictyon poshanense* Ozaki 1938. *Pachystylodictyon fragosum* Nestor is the only Estonian Late Ordovician form referred to the genus (Nestor 1964); and it also lacks pillars and would seem more correctly allied to *Pseudostylodictyon* or perhaps to *Rosenella*. It is to be hoped that pillars will eventually be found in *Pachystylodictyon ungeri* to validate this now well-accepted genus, characterized by the presence of both cysts and laminae, as well as pillars and denticles (Nestor, 1964; Mori 1969; Kapp & Stearn 1975). Nestor's (1976) reference to the division of thick cyst walls into a 'basic plate' and a 'covering plate' as a diagnostic feature of *Pachystylodictyon* seems totally unacceptable. The genus (Fig. 4B-F) differs from *Pseudostylodictyon* in having pillars, from *Labechia* in having laminae, from *Labechiella* in exhibiting both denticles and cysts, and from *Rosenella* in showing both pillars and laminae.

Nestor's (1976) tentative assignment of *Rosenella woyuensis* Ozaki 1938 to *Pachystylodictyon* seems unjustified on the grounds that Ozaki's (1938) type specimens from China, and the New South Wales material of *R. woyuensis* (see Webby, 1969),

Fig. 4. *Pseudostylodictyon* aff. *poshanense* Ozaki 1938; vertical section of SUP 26235 from the lower part of the Cliefden Caves Limestone west of Boonderoo shearing shed, central western New South Wales; $\times 5$. B-C, *Pachystylodictyon* sp. A from the Mjøsa Limestone north of Bergvika, Norway; PMO 97112; $\times 5$. B transverse section. C, vertical section. D-F, *Pachystylodictyon* sp. B, $\times 5$. D, vertical section of UTGD 94649 from the middle part of the Gordon Limestone Subgroup just below the *Pliomerina* siltstones, Mole Creek, Tasmania. E, vertical-oblique section of UTGD 25374 from Gordon Limestone Subgroup at Gunns Plains. F, transverse section of UTGD 94648 from same horizon and locality as Fig. 4. D. G-H, new genus allied to *Stromatocerium* from Mjøsa Limestone south of Bergvika, Norway; PMO 97113, $\times 5$. G, vertical section. H, tangential section.

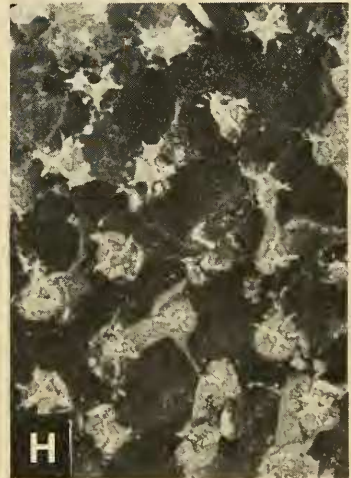
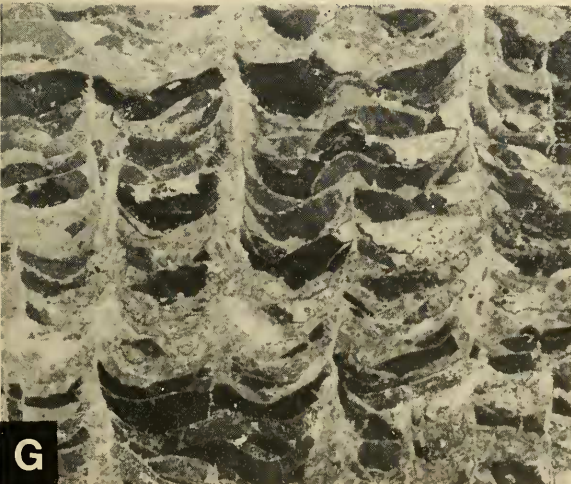
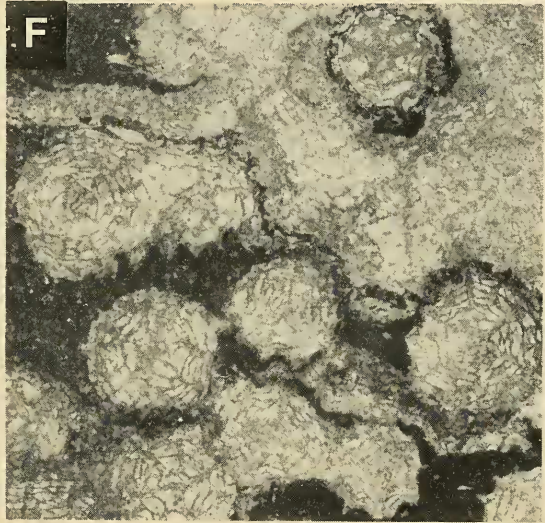
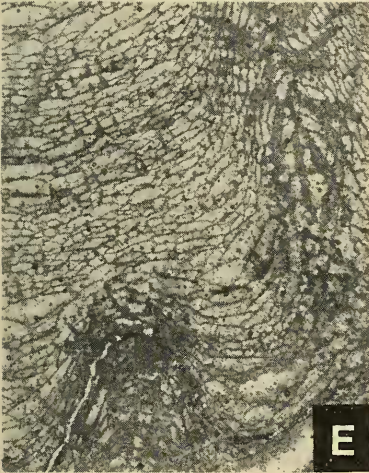
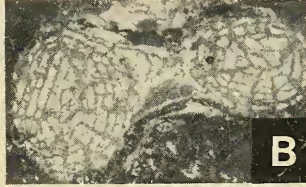
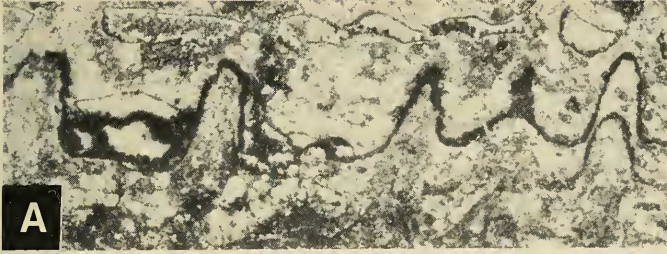


exhibit large and small cysts (but no laminae) and denticles (but no true pillars). Occasional pillars are exhibited by *Rosenella amzassensis* Khalfina 1960a from the late Ordovician of Gornaya Shoriya and in material from the Moiero River of northern Siberia, both included by Nestor (1976) in his conception of *woyuensis*. It would seem preferable to group the Gornaya Shoriya and Moiero material in *amzassensis* and, despite the lack of well defined laminae, tentatively assign it to the genus *Pachystylostroma*. This species is not synonymous with *Rosenella woyuensis*.

(viii) *Stromatocerium* Hall 1847 — The genus resembles *Labechiella* but the pillars have angular, meandriform, stellate or flanged outlines, as seen in tangential section. The cyst plates are frequently but not always flattened into long-low cysts or laminae. Denticles are not present. Pillars of virtually all described species of *Stromatocerium* appear to be secondarily altered, possibly mainly by diagenetic leaching of the interiors of the pillars, and subsequent infilling by sparry calcite. Even the upwardly protruding tips of the pillars on the upper surfaces of the coenostea are replaced and filled with sparry calcite (Fig. 1C-F). Had the pillars been originally hollow as suggested by Nestor (1964; 1976) and Kaźmierczak (1971), they would not have been preserved as upwardly protruding tubercles in the sediment. To explain the formation of sparry calcite filled 'hollow pillars' or 'walless rods' requires a process of diagenetic alteration (Kapp & Stearn, 1975) probably involving selective subaerial leaching of solid pillars and subsequent infill with sparry calcite. It follows that the irregular to angular pillars of many forms may have been derived by secondary processes from large, solid, possibly originally rounded vertical elements of *Labechia* or *Labechiella* type, suggesting that *Stromatocerium* at best should be viewed as a form genus.

Nestor (1976) has recently recommended that the conception of the genus be restricted to representatives of the *S. rugosum* group, and that members of the *S. michiganense* group should be included in a separate genus. Pillars of the first type are 'hollow', wall-like, of variable cross-sectional shape, usually radiating from centres which may include associated mamelons (group A of Fig. 10). Pillars of the second type are thin, complexly bent and intermeshed vertical plates, not radiating outward from centres (group C of Fig. 10). A third group, the *S. canadense* group, were assigned by Nestor (1976) to the genus *Cystistroma* Etheridge 1895. Nestor's *S. canadense* group has at least one form exhibiting denticles and therefore strictly equatable with *Cystistroma* but there are others with 'hollow', rounded to angular pillars and no denticles which should be included in a separate group (group B of Fig. 10). A good example is the new species (Fig. 1C-F) presently under description from the lower part of the Gordon Subgroup in Tasmania (Webby, in press b).

In their classification of stromatoporoids, Khalfina & Yavorsky (1973) introduced the genus *Platiferostroma* to accommodate forms with *Stromatocerium*-like pillars and upwardly convex cysts (like the type species of *Labechia*). They assigned *Stromatocerium huronense* Billings, described by Parks (1910) from the Late Ordovician of North America, to the new genus. However, this species was subsequently revised by Galloway & St. Jean (1961) and assigned in part to *Labechia huronensis* (Billings) and in part to *Stromatocerium granulosum* (James). The former has round pillars and the latter does not have conspicuously arched cyst plates. The former should be retained in *Labechia* and the latter in *Stromatocerium*. The genus *Platiferostroma* (with its type species *Stromatocerium hydridium* Dong 1964) is thus best regarded as restricted to the lowest levels (Etremoungtian) of the Carboniferous.

(ix) *Cystistroma* Etheridge 1895 — Like *Stromatocerium* it typically exhibits a

coarse-textured structure of large pillars and cysts, but the pillars have a rounded to irregular or serrated outline in tangential section, and tiny denticles occur on upper surfaces of cyst plates and in places on outer surfaces of the large pillars (Fig. 3E). It is likely that the large pillars of *Cystistroma* were derived from mamelon columns of a form like *Pseudostylodictyon poshanense* Ozaki (Fig. 4A), as outlined previously (Webby, 1969). There is little likelihood, owing to the markedly different order of magnitude of size difference between the pillars and denticles, of the pillars being derived by superposition of the denticles as in other labechiids such as *Labechia* and *Pachystylostroma* (Kapp & Stearn, 1975). *Stromatocerium canadense* Nicholson & Murie 1878 from the Middle Ordovician of eastern North America (and perhaps the Estonian counterparts including *S. sakuense* Nestor 1964) should be assigned to *Cystistroma*. North American specimens have denticles on the upper surface of cyst plates and 'short, spine-like flanges' on the pillars (Parkes, 1910; Galloway & St. Jean, 1961, p. 60).

(x) New genus allied to *Stromatocerium* — The distinctive *Stromatocerium*-like morphology with long, slender, 'composite' vane-like pillars and denticles (Fig. 4G-H) is currently being described as a new genus based on material from the Middle Ordovician Mjøsa limestone of Norway (Webby, in press, a). *Pachystylostroma* and the related *Stylostroma* Gorsky 1938 (also including forms previously assigned to *Pseudolabechia* Yabe & Sugiyama 1930 but now excluded because *Pseudolabechia* proved to be an actinostromatid not a labechiid — see Mori, 1969; 1970) both exhibit well developed, upwardly and outwardly radiating pillars within the mamelon columns (*Pachystylostroma* also has them in other parts of the coenosteum). In longitudinal section the pillars may be fused to form a vertically continuous, vane-like structure — see, for example, *Stylostroma gracile* (Yavorsky, 1957, pl. 19, figs 1-3) — while in tangential section they exhibit a stellate pattern of outwardly radiating pillars centred on the axis of the mamelon. The 'composite' vane-like pillars of the new genus appears to have been derived from former mamelon columns. To what extent these structures are primary, and to what extent they are modified by secondary diagenetic alteration processes is uncertain.

(xi) *Lophiostroma* Nicholson 1891 — Nicholson (1891), Kühn (1927; 1939), Lecompte (1956) and Yavorsky (1962) all assigned *Lophiostroma* to labechiids, but Galloway (1957) preferred a grouping with the actinostromatids on the basis of the thickened skeletal tissue and laminae inflected into columns and, more recently, Khalfina & Yavorsky (1973) classified *Lophiostroma* with the clathrodictyids. Nestor (1966b) and Mori (1970), excluded the genus from the labechiids, assigning it instead to the family Lophiostromatidae Nestor 1966b — more recently (Nestor 1974; 1976) to the superfamily Lophiostromatacea — on the grounds of it having undifferentiated skeletal tissue completely filling the interior of the coenosteum. The series of sharply undulating 'laminae' (possibly representing pauses of growth rather than true laminae) defines the positions of the conical pillar-like structures, seen as papillae on the upper surface of the coenosteum. The papillae in the type species of *Lophiostroma*, *L. schmidtii* (Nicholson) from the Silurian of Gotland (Mori, 1970, pls 19-20), are remarkably similar in size and appearance to those of the type species of *Labechia*, *L. conferta* (Lonsdale) from the Silurian of England and Gotland. The only named Ordovician species closely resembling the type species is *Lophiostroma shantungensis* Yabe & Sugiyama 1930 from the Middle Ordovician of China. Its coenosteum is almost completely filled with poorly differentiated skeletal tissue, but there are traces of pillars with upwardly-directed cone-in-cone structure, and a few large, calcite-filled cysts. This species appears to be unquestionably a labechiid, possibly derived by massive thickening of its skeletal tissue from a *Labechiella*, or a

Labechia. *Lophiostroma elandiense* Khalfina 1960a from the Late Ordovician of the Altai region seems to represent a rather poorly preserved *Labechiella*.

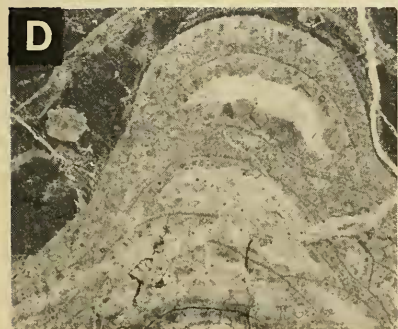
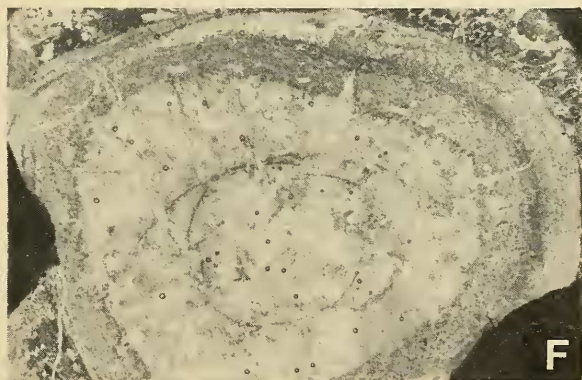
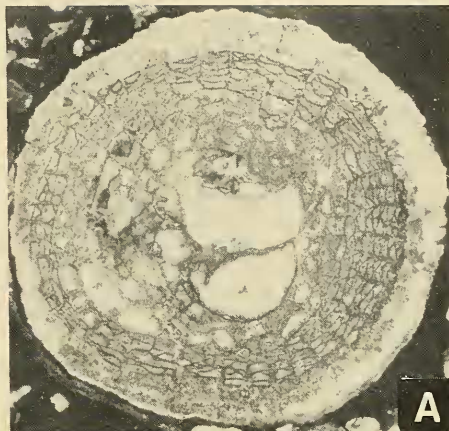
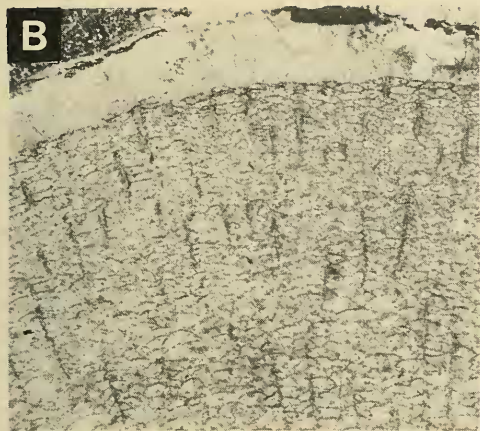
(xii) *Dermatostroma* Parks 1910 — This problematical, thin, encrusting labechiid typically exhibits a papillose upper surface appearance like a *Labechia* or *Lophiostroma* (see illustration of *D. scabrum* in Galloway & St. Jean 1961, pl. 13, fig. 1), but has a less well defined internal structure. The genus seems to be restricted to the Middle-Late Ordovician horizons of North America (Parks 1910; Galloway & St. Jean 1961). The first group has a few laminae and pillars, the second, radially crystalline prisms (possibly representing much thickened pillars) and the third exhibits a structureless mass of calcite crystals. The first group may be allied to *Labechiella*, the second to *Lophiostroma* and the third is of uncertain affinities (but has a constant encrusting association on species of *Aulacera*). Nestor (1974; 1976) has included *Dermatostroma* in the family Lophiostromatidae (and superfamily Lophiostromatacea) thus separating it from other labechiids like *Labechiella*. In spite of its need for revision, this genus should continue to be associated with the labechiids.

(xiii) *Sinodictyon* Yabe & Sugiyama 1930 and *Ludictyon* Ozaki 1938 — Both forms come from the Middle Ordovician of China. *Sinodictyon* is a fasciculate to cylindrical form with large, denticled cysts axially, and rows of smaller, long-low cysts with denticles and pillars laterally. The morphology of the axial zone resembles *Rosenella*, and the lateral zone, a *Labechia* of the *L. prima*-*L. eatoni* type. Galloway (1957) included the genus *Ludictyon* Ozaki in synonymy with *Sinodictyon*, but *Ludictyon* has a more-or-less broadly cylindrical coenosteum with less well defined axial and lateral zones, a pattern of alternating large and small cysts in the axial zone, rows of smaller cysts laterally, and denticles in both axial and lateral zones (Ozaki 1938). It does not seem to be a convincing junior synonym of *Sinodictyon*. Apart from its broad columnar form, *Ludictyon* exhibits close morphological similarities with laminar-hemispherical *Rosenella*, and appears to represent an earlier stage in evolutionary development from a *Rosenella*-type ancestor than does *Sinodictyon*.

(xiv) *Cryptophragmus* Raymond 1914, *Thamnobeatricea* Raymond 1931 and *Cladophragmus* Raymond 1931 — These slender North American Middle Ordovician forms have been grouped together as representatives of a single genus, *Cryptophragmus* by Galloway (1957) and Galloway & St. Jean (1961), even though there are distinctive differences between them. As Raymond (1931) noted, *Cryptophragmus* is unbranched, *Thamnobeatricea* has lateral branching and *Cladophragmus* exhibits bifurcating branches. *Cryptophragmus* has an axial column with a narrow lateral zone, and an outer sheath with the structure of *Labechia* which is rarely seen in continuity with the axial column. It needs to be resolved whether *Cryptophragmus* represents the growth of one or more than one organism. *Cladophragmus*, on the other hand, has no lateral zone or sheath.

The relationships of these slender cylindrical genera (Fig. 5C) to laminar-

Fig. 5. A, *Alleymodictyon nicholsoni* Webby 1971 from the Gerybong Limestone Member, Daylesford Limestone (Bowen Park Group) at The Ranch, Bowen Park area, central western New South Wales; transverse section of holotype SUP 34170, $\times 4$. B, *Aulacera* sp. A from the uppermost part of the Gordon Limestone Subgroup at The Den, Mole Creek area, Tasmania; transverse section of outer zone of large specimen, UTGD 94651, $\times 4$. C, *Cryptophragmus*? sp. from the Lower Limestone Member of the Benjamin Limestone (Gordon Limestone Subgroup) in the Florentine Valley; vertical section of UTGD 94654, $\times 4$. D, *Rosenella* sp. from the Gordon Limestone Subgroup at Ida Bay; vertical section of UTGD 94650, $\times 4$, showing prominent mamelon-like upgrowth. E, *Aulacera* sp. B from the uppermost part of the Gordon Limestone Subgroup at The Den, Mole Creek area; vertical section of UTGD 94652, $\times 2$. F-G, *Aulacera* sp. C from the upper part of the Gordon Limestone Subgroup at Gunns Plains; $\times 2$. F, transverse section. G, vertical section.



hemispherical labechiids are not clearly established. They may have evolved from mamelon-like columns extending upwards off a laminar-hemispherical base, but such bases have not yet been found. They may have been derived from a strongly mammillated representative of *Cystostroma*, *Pseudostylodictyon* or *Rosenella* with its mamelons exhibiting large 'axial' cysts.

(xv) *Alleynodictyon* Webby 1971 — The genus (Fig. 5A) appears to be more closely related to *Cryptophragmus* and its allies than to *Sinodictyon* and *Ludictyon*. It differs from all other cylindrical labechiids by exhibiting blade-like pillars. Representatives of *Stromatocerium* and the *Stromatocerium*-like new genus with blade-like pillars provide a clue to the possible mode of derivation of the pillars of *Alleynodictyon*. In the new genus, the outwardly radiating, 'composite' vane-like pillar structure (Fig. 4 G-H) seems to have formed from the many upwardly and outwardly inclined, small pillars fusing in continuous vertical rows and linking axially. Each such 'composite' pillar seems to have been derived at the axis of a former, *Pachystylostroma*-like mamelon column by apparent coalescence of numerous small pillars (Fig. 4 B-F). *Alleynodictyon* (if the cylindrical branches are viewed as modified mamelon columns) have a differentiated coenosteum with a lateral zone and an axial column. The small pillars which are similarly formed by fusion into vertical rows are however confined to the lateral zone. They resemble septa in rugose corals.

(xvi) *Aulacera* Plummer 1843 (= *Beatricea* Billings 1857) — The coenosteum of *Aulacera* is unbranched, and it has a relatively wider lateral zone than in other cylindrical labechiids. The axial column is usually sharply differentiated from the lateral zone, and exhibits a series of large, superposed cysts; the lateral zone shows rows of imbricated, smaller cysts with pillars distributed, usually sporadically, in the outer part (Fig. 5B, E-G). Specimens of large dimensions have been recorded from the Late Ordovician of Anticosti Island (Twenhofel 1928). In places along the coast of Anticosti, they occur so thickly 'as to resemble piles of petrified logs'. They protrude like hollowed trunks 'suggesting small cannon projecting from a wall' (Twenhofel, 1927, p. 105) in a cliff face on Anticosti, appropriately named Battery Point. Mostly they lie in the plane of bedding, but occasionally a specimen is seen to be orientated in a vertical or upright (?growth) position. Attachment bases have not been positively confirmed.

Most workers (Schuchert 1919; Twenhofel 1927; Yavorsky 1955; 1957; Galloway & St. Jean 1961) have interpreted *Aulacera* as having had an erect life orientation, growing up vertically off an attachment base. However, Copper (1974, p. 379) has argued that *Aulacera* may have rolled around on the sea floor instead of growing vertically! In preferring a vertical mode of growth, it should be emphasized that only a relatively small part of the total preserved length of the coenosteum (observed to a maximum of 5 m) — the apical growing area of Webby (1971) — may have projected above the sea floor at any one time, and upward growth may have kept pace with the adjoining sediment accumulation. However, a period of intense erosion and bodily transport of these giant columnar 'structures' would have been required to reorientate them into their final resting place, in the plane of bedding.

Aulacera, though apparently confined to the Richmond (Late Ordovician) of North America first appears in stratigraphically lower levels in Tasmania (possibly equatable with the Eden or Maysville), and possibly from still lower horizons in China — *Aulacera peichuangensis* Ozaki 1938 being recorded from the Middle Ordovician ('Blackriver' or 'Trenton') of China.

(b) *Family Clathrodictyidae*

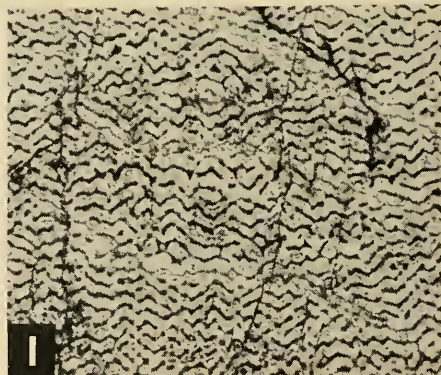
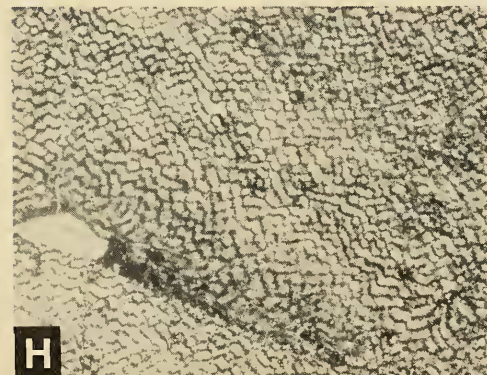
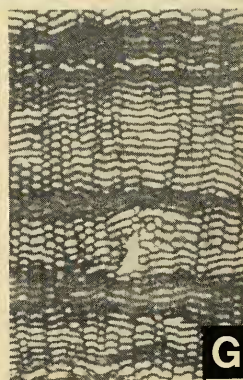
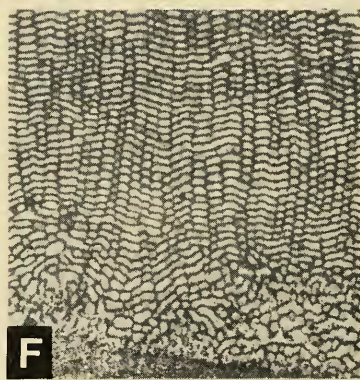
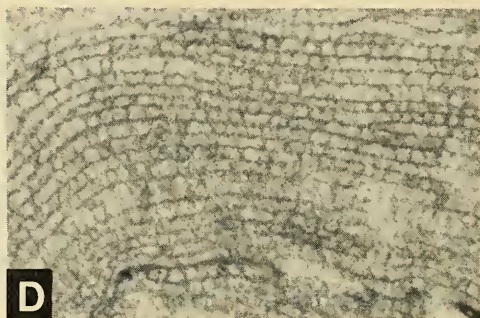
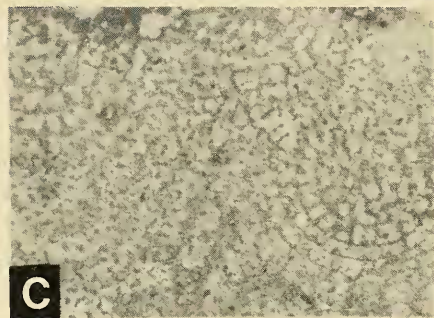
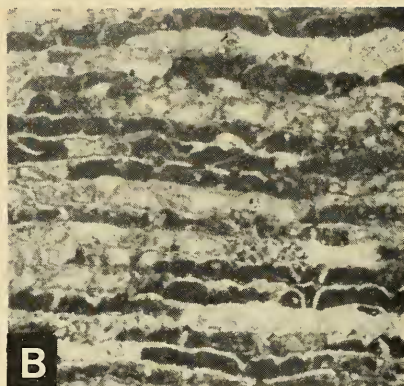
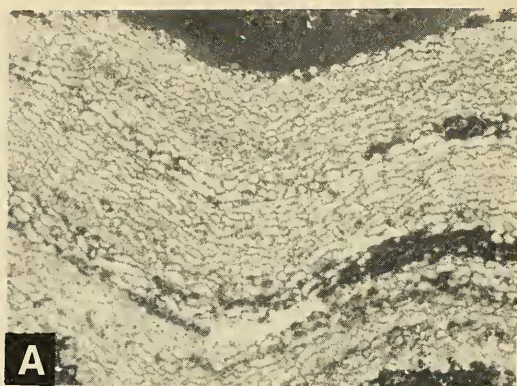
Galloway (1957) in an outline of the phylogeny of Stromatoporoidea regarded

the Labechiidae with their simple morphology and earliest appearance as ancestral directly or indirectly to all other stromatoporoid families. Galloway viewed the Clathrodictyidae as having evolved from a member of the labechiids in the Late Ordovician, the overlapping or imbricated cysts of labechiids being replaced by 'the side-by-side placing of the cysts' of clathrodictyids. A similar derivation of clathrodictyids ('laminar' stromatoporoids) from labechiids ('vesicular' stromatoporoids) through a succession of developmental stages from Late Ordovician to Early Silurian time is inferred by Nestor (1966a). He depicted a trend from a *Cystostroma*-like ancestor composed of imbricate, upbranched cyst plates, but not arranged in orderly rows, to *Clathrodictyon vormsiense* Riabinin from the Late Ordovician (Vormsi horizon) of Estonia with regular rows of long-low cyst plates, to more typical representatives of the genus, in the very topmost beds of the Ordovician (Porkuni horizon of Estonia) — forms such as *Clathrodictyon gregale* Nestor and *C. zonatum* Nestor with irregular laminae. Bogoyavlenskaya (1969) and Kaźmierczak (1971) have made similar suggestions regarding the derivation of 'laminar' stromatoporoids from *Cystostroma*. It is perhaps significant that both labechiids and clathrodictyids typically exhibit a microstructure of non-porous, speckled, compact tissue (Stearn 1966).

Neither Galloway, Nestor, Bogoyavlenskaya nor Kaźmierczak explained precisely how the pillars of *Clathrodictyon* were formed. Typically confined to a single interlaminar space (Stearn, 1966), the pillars are not as Galloway (1957) contended, strictly the downward continuations of the edges of the cysts, otherwise the intersected cyst walls would appear as circles or polygonal outlines in tangential sections (Khalfina & Yavorsky 1967). The funnel-like (or inverted cone-shaped) pillars of some species of *Clathrodictyon* (Stearn, 1966; Stearn & Hubert 1966) may reflect an origin of the pillars from intersections of downwardly-inflexed cyst plates. However, usually the pillars show little or no trace of associated downwardly-inflexed cyst tissue. If *Clathrodictyon* evolved from the labechiids then the 'labechiid-type' cyst walls must have broken down or failed to calcify. The regularity in the spacing of pillars may be explained by the pillars having been derived at points of intersection of former downwardly-inflexed cysts.

(i) *Clathrodictyon* Nicholson & Murie 1878 — Characteristically *Clathrodictyon* is a Silurian genus with a widespread and abundant distribution (Nestor 1964; 1966b; 1976; Birkhead 1967; Mori 1969; 1970; Bolshakova 1973). Its Late Ordovician record is more restricted but not confined to Estonia and Anticosti Island as previously indicated by Galloway (1957). Nestor (1964) described some five species from Estonia, and proposed two of them as name-bearers from his Late Ordovician stromatoporoid zones. Webby & Banks (1976) have recorded an additional four species from the Late Ordovician (probably about Late Caradoc in age) of Tasmania (Fig. 6 C-D). One Tasmanian species *C. idense* is notable among Ordovician forms for exhibiting dissepiments which link the pillars and subdivide the galleries. Species allied to the Estonian forms have also been reported by Webby (1969) from the Late Ordovician of New South Wales (Fig. 6A-B), and by Bogoyavlenskaya (1973) from the western Urals.

(ii) *Ecclimadictyon* Nestor 1964 — The genus has a similar distribution and stratigraphic range to that of *Clathrodictyon*. It is related to *Clathrodictyon* but differs in exhibiting zigzag-shaped laminae, and relatively less conspicuous pillars. Although not clearly developed in all species, the pillars are confined to interlaminar spaces and tend to be alternating, not superposed; they formed from downwardly inflected laminae seemingly also at intersections of 'cyst plates'. A distinctive orderly



meshwork is represented in tangential section by the pattern of distribution of the pillars and intersecting downwardly inflected chevron-shaped laminae.

Nestor (1974) has inferred a derivation of *Ecclimadictyon* either from *Clathrodiction* or, less certainly, directly from *Cystostroma*. In the Estonian successions, the first clathrodictionyids to make their appearance are *Clathrodiction vormsiense* and *C. microundulatum* whereas in New South Wales *Ecclimadictyon nestori* (Fig. 6H) first appears stratigraphically well below the first representative of *Clathrodiction* (see Webby & Morris 1976, fig. 1). It comes in, indeed it defines, the base of Fauna 2, at a stratigraphical level which is no later than Early Eastonian (= middle Caradoc, or late Middle Ordovician in terms of North American or Baltic successions).

Late Ordovician species of *Ecclimadictyon* include *E. porkuni* (Riabinin) and *E. koigiense* Nestor from Estonia (Nestor 1964), *E. geniculatum* Bogoyavlenskaya 1973 from the Urals, *E. amzassensis* (Khalfina) from south-west Siberia and New South Wales (Khalfina 1960a; Webby 1969), *E. nestori* Webby 1969, *E. cribratum* Webby & Morris 1976 from New South Wales, and *E. undatum* from Tasmania (Webby & Banks 1976). Both the Estonian species are from the uppermost (Porkuni horizon) part of the Ordovician, and differ from the others in exhibiting dissepiments. Two other species are especially distinctive — *E. amzassensis* exhibits overall vertical continuity in alignment of zigzag-shaped rows of pillars (Fig. 6E-G), and *E. cribratum* has patches of horizontal tissue with 'hexactinellid' rod-like radial processes (Fig. 6I).

(iii) *Plexodiction* Nestor 1966b — Nestor (1966b), Stearn (1969) and Bogoyavlenskaya (1973) have regarded the genus *Plexodiction* as restricted to Late Silurian strata. However, *P. ?cascum* Webby & Morris 1976 from the Late Ordovician of New South Wales (Fig. 7D), is a species with close morphological similarities to the late Silurian representatives of the genus, and suggests a much earlier derivation of *Plexodiction* from *Ecclimadictyon* than previously thought. It may be significant that a *Plexodiction*-like structure develops in mamelon-like upgrowths of the coenostea of some of the earliest known species of *Ecclimadictyon* and *Clathrodiction* (see Webby & Banks, 1976, p. 131, pl. 2, fig. 5 and Webby & Morris 1976 p. 132, Fig. 5D).

(c) Family Cliefdenellidae

Webby (1969) and Webby & Morris (1976) have discussed relationships between Cliefdenellidae and other stromatoporoid groups. The family contains only the one genus, *Cliefdenella* Webby 1969. No other Ordovician stromatoporoid exhibits such a complex association of primary laminae with denticles on upper surfaces, dissepiments and a ramifying meshwork of horizontal astrorhizal canals filling interlaminar spaces,

Fig. 6. *Clathrodiction* cf. *microundulatum* Nestor 1964 from the Clearview Limestone Member of the Ballingool Limestone (Bowen Park Group), near Malachi's Hill, central western New South Wales; vertical section of SUP 29133, $\times 5$. B, *Clathrodiction* aff. *mammillatum* (Schmidt 1858) from the Davy's Plains Limestone Member of the Daylesford Limestone (Bowen Park Group) at Quondong, central western New South Wales; vertical section of SUP 43173, $\times 10$. C-D, *Clathrodiction plicatum* Webby & Banks 1976 from the uppermost part of the Gordon Limestone Subgroup in Tasmania, $\times 10$. C, tangential section of holotype UTGD 94626 from roadside locality leading to main quarry west of The Den, Mole Creek. D, vertical section of paratype UTGD 94629 from The Den. E-G, *Ecclimadictyon amzassensis* (Khalfina 1960a) from the upper part of the Cliefden Caves Limestone at The Island, Cliefden Caves, central western New South Wales, $\times 5$. E-F, tangential and vertical sections of SUP 26206. G, vertical section of SUP 26207. H, *Ecclimadictyon nestori* Webby 1969 from the upper part of the Cliefden Caves Limestone at The Island; vertical section of paratype SUP 26200, $\times 10$. I, *Ecclimadictyon cribratum* Webby & Morris 1976 from limestone breccia at the top of the Malongulli Formation, near Malongulli Trig., central New South Wales; vertical section of holotype SUP 78266, $\times 10$.

and vertical astrorhizal columns with associated updomed laminae, astrorhizal canals and vertical spine-like elements (Fig. 7A-C). It resembles a *Plexodictyon*-type structure (Webby & Morris 1976) with the addition of the complex astrorhizal system and 'tube-like' pillars. The vertical elements of the coenosteum — the 'tube-like' pillars and the astrorhizal columns — seem to retain their independence as discrete units and never appear to exhibit interconnection one with the other. Origins of this group are obscure. *Cliefdenella* makes its first appearance in beds of Fauna 2 (about middle Eastonian or, in North America terms, 'Trenton') of the N.S.W. succession, only about 100 m stratigraphically above the first incoming of clathrodictyids (Webby & Morris, 1976). The genus is known through a stratigraphical range in N.S.W. from the middle Eastonian to early Bolindian (Faunas 2-3 of Webby 1969), and from the Late Ordovician of Salair in south-west Siberia (Khalfina & Yavorsky 1974).

STRATIGRAPHIC DISTRIBUTION

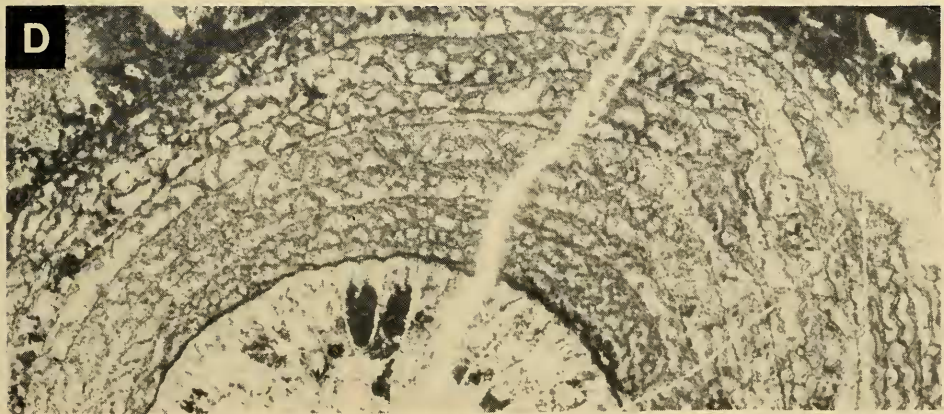
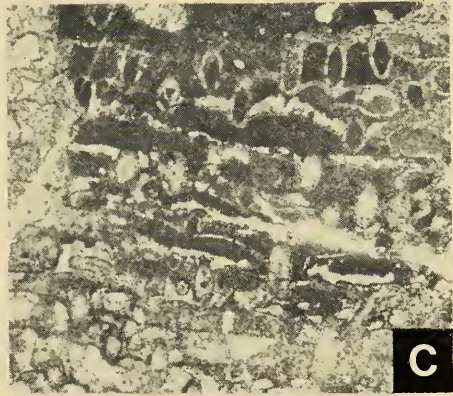
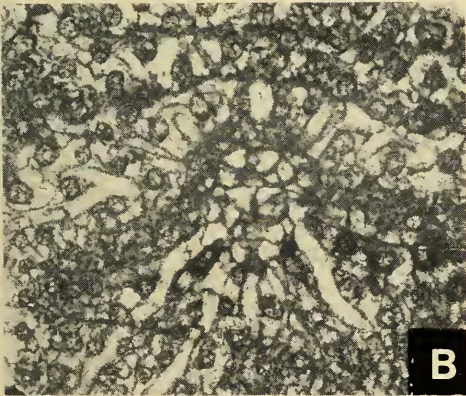
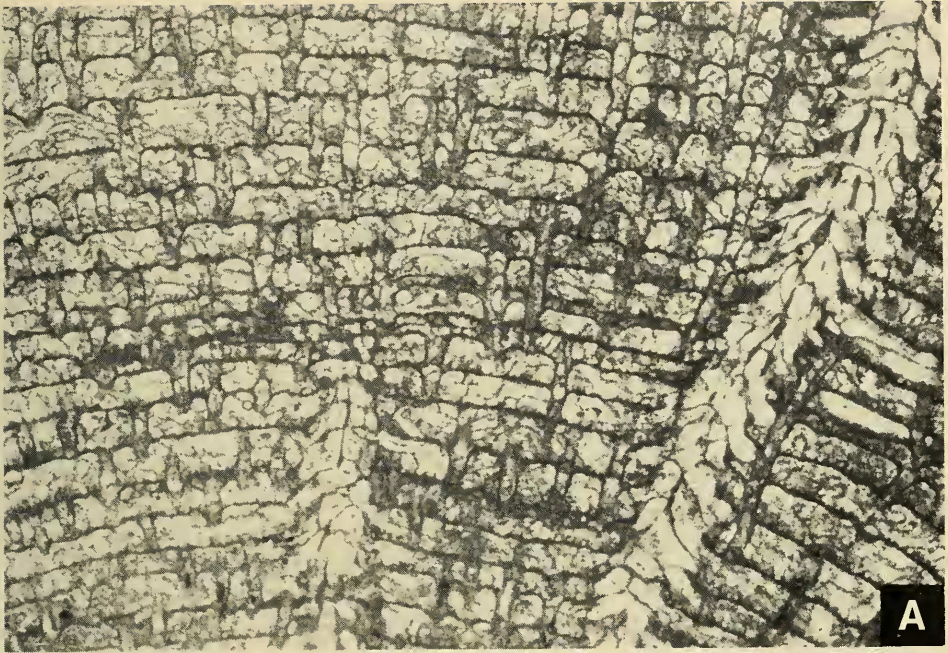
(a) *Australia*

(i) *New South Wales*. — Three biostratigraphically distinct coral and stromatoporoid faunas (Faunas 1, 2 and 3) have been recognized from the Late Ordovician (Gisbornian-Bolindian) limestone successions of central western New South Wales (Webby 1969; 1971; 1975). The labechiids, *Pseudostylodictyon* aff. *poshanense* Ozaki, *Stratodictyon ozakii* Webby, *S. columnare* Webby, *Rosenella woyuensis* Ozaki, *Labechiella regularis* (Yabe & Sugiyama), *Cystistroma donnellii* Etheridge and *Alleynodictyon nicholsoni* Webby appear in Fauna 1 (Fig. 8), of probable late Gisbornian age. In terms of the North American sequence, this level would be roughly equivalent to a late Porterfield? or early Wilderness age (i.e., in the older nomenclature, a 'Blackriver' age). This is the oldest stromatoporoid fauna known from New South Wales; and it already exhibits considerable diversity from the basic labechiid stock.

The first appearance of clathrodictyids defines the base of Fauna 2, in sequence some 94 m above the top of the lower, thinly bedded member of the Cliefden Caves Limestone (Webby & Morris, 1976). On the basis of present correlations, these clathrodictyids (*Ecclimadictyon nestori* Webby and *Plexodictyon* ? sp.) probably first appeared about the beginning of the Eastonian and the first cliefdenellids in the middle Eastonian. The stratigraphic distribution of the Ordovician clathrodictyid and cliefdenellid stromatoporoids was shown in fig. 1 of Webby & Morris (1976). The labechiid component of Fauna 2 includes *Cystostroma cliefdenense* Webby, *Pseudostylodictyon inaequale* Webby and *Labechiella variabilis* (Yabe & Sugiyama). *Cystostroma cliefdenense* seems to be in no way closely linked or related to the first clathrodictyids. Indeed the clathrodictyids actually appear stratigraphically below the first occurrences of *C. cliefdenense*. In terms of North American successions, Fauna 2 would equate with the 'Trenton' (Fig. 8), or in the revised terminology of Sweet & Bergström (1976), the Rocklandian-Shermanian.

Fauna 3 spans an interval from the late Eastonian to the early Bolindian, broadly equivalent to the Eden-Maysville interval of North America (Fig. 8). The

Fig. 7. A-C, *Cliefdenella etheridgei* Webby 1969 from the upper part of the Cliefden Caves Limestone, The Island, Cliefden Caves area, central western New South Wales; $\times 5$. A, vertical section of holotype SUP 24157. B, tangential section of paratype SUP 24154. C, oblique-vertical section of paratype SUP 24156. D, *Plexodictyon? cascum* Webby & Morris 1976 from the Clearview Limestone Member of the Ballingool Limestone (Bowen Park Group) of central western New South Wales; vertical section of paratype SUP 77277, $\times 7.7$. Note the association with the rugosan *Palaeophyllum patulum* McLean & Webby 1976.



stromatoporoids occur mainly in the upper part of the respective limestone successions at Bowan Park and elsewhere, and may represent a mainly 'early Bolindian' fauna. They include cliefdenellids, clathrodictyids (including *Plexodictyon? cascum*) and the labechiid, *Pseudostylodictyon inequale*. No stromatoporoids have been found in higher Ordovician horizons of New South Wales.

(ii) *Tasmania*. — Carbonates of the Gordon Subgroup accumulated through much of Ordovician time on the Tasmanian Shelf (Banks, 1962; Webby 1976; 1978). Only the clathrodictyid stromatoporoids from the upper part and labechiids from the lowest part of the sequence have so far been studied in detail (Webby & Banks, 1976; Webby, in press b). The bulk of the fauna consists of labechiids (no cliefdenellids are known), and comprises a very diverse and abundant component of the total biota. Corbett & Banks (1973) have outlined the general faunal and floral succession in the Gordon Subgroup of the Florentine Valley area as consisting of some eight stratigraphically distinct 'faunas', probably ranging from about Castlemainian (late Arenig) to early Bolindian. The first three 'faunas' lack stromatoporoids but the fourth contains *Stromatocerium* in an assemblage with *Maclurites* and *Girvanella*. It occurs in the Cashions Creek Limestone of probable Darriwilian age — approximately equivalent to middle-late Chazy of North America. The stromatoporoid faunas from this horizon to the top of the subgroup (from the fourth to eighth 'faunas' inclusive) are more complete and better preserved in the Mole Creek section than in the Florentine Valley.

The first stromatoporoids to appear in the basal part of the Gordon Subgroup of the Mole Creek area are *Stromatocerium*, *Stratodictyon* and *Labechia* (Figs 1D-F; 2A-B, D). Stratigraphically higher, in the 'Lichenaria' beds, exposed in the cliffs above Sassafras Creek, *Labechia* (Fig. 2E-F) is exposed in latilaminar, dome to sheet-like 'colonies' up to 550 mm across and 220 mm in height. *Rosenella* and a branching cylindrical form, possibly *Cryptophragmus*, make their appearance towards the top of the cliffs. Still higher the first *Pachystylostroma* comes in. These occurrences together with the first appearances of *Tetradium* and *Eofletcheria* suggest a correlation with the earliest N.S.W. coral/stromatoporoid fauna (Fauna 1).

Stratigraphically much higher, immediately beneath the *Pliomerina* siltstones, the stromatoporoids include abundant *Pachystylostroma* (Fig. 4D, F) and less common *Labechia*, *Labechiella* and *Rosenella*. *Palaeophyllum* and heliolitids have been observed from this part of the sequence indicating a correlation with N.S.W. Fauna 2. Above the *Pliomerina* siltstones, the faunas are rather sparse and the record of stromatoporoids incomplete. However, towards the top of the sequence of the Gordon Subgroup, at The Den and in the vicinity of the large working quarry farther west, there is a rich stromatoporoid fauna comprising *Labechia*, *Labechiella*, *Rosenella*, *Aulacera* (Fig. 5B, E) and the clathrodictyids *Ecclimadictyon undatum* Webby & Banks, *Clathrodictyon plicatum* Webby & Banks, *C. molense* Webby & Banks and *C. sp.* The fauna is associated with abundant corals including favositids, halysitids, *Favistina* and other characteristic elements of Fauna 3. It is very tentatively correlated with the Eden-Maysville of North America (Fig. 8), despite the occurrence of *Aulacera*, which tends to be restricted to the Richmond of North America (Galloway & St. Jean 1961).

Appearances of Ordovician stromatoporoid genera in Australian successions are depicted in Fig. 8. The maximum period of diversification of stocks seems to have occurred in the Gisbornian, with the appearance of Fauna 1. The species of *Stromatocerium*, *Stratodictyon* and *Labechia* in the lowest part of the limestone at Mole Creek are distinctly different forms (Figs 1D-F; 2A-B, D) and cannot easily be linked through intermediate forms back to a common ancestor. The species of

Stratodictyon and *Labechia* may have evolved from an early Chazy representative of *Pseudostylodictyon*, like *P. lamottense*, thought by Kapp & Stearn (1975) to be the oldest North American stromatoporoid, but *Pseudostylodictyon* has not been found in the lowest stromatoporoid-bearing beds of the Gordon Subgroup of Tasmania. The species of *Stromatocerium*, has no known progenitor unless it is interpreted as having descended from Khalfina & Yavorsky's (1974) supposed Early Cambrian *Stromatocerium* of the Kuznetsky Alatau region, Siberia (see later discussion, p. 113). From the initial *Stromatocerium*, *Labechia* and *Stratodictyon* stocks in these lowest horizons of the Gordon Subgroup, it would not have been difficult to derive the more diverse Fauna 1 assemblage.

(b) North America

Kapp & Stearn (1975) have traced the evolutionary history of the oldest stromatoporoids in North America. They have interpreted *Pseudostylodictyon lamottense* which first appears in the Day Point Formation (zone 1) of the Chazy Group, and has 'denticled laminae and large irregular cysts', as representing the earliest stage of stromatoporoid evolution. Diversification from this ancestral stock took place along two main paths, typified by the genera *Labechia* and *Pachystylstroma*. Both genera make their appearance in the Crown Point Formation (zone 2) of the Chazy Group — *Labechia eatoni*, *L. prima* and *Pachystylstroma goodsellense*, the first to exhibit vertical pillars supposedly secreted to strengthen the coenosteum. In the next stage of evolutionary development through the middle-late Crown Point and Valcour Formations (mid-late Chazy) a further two species of *Labechia* and three species of *Pachystylstroma* appeared, presumably derived from the main stock of *L. eatoni* and *P. goodsellense*.

The genus *Cystostroma* which is formed solely of cysts without laminae or pillars has as its type species *C. vermontense* originally described from the Crown Point Formation, and considered by many workers, most notably by Galloway (1957) and Nestor (1964; 1966a), as the most primitive stromatoporoid. Unfortunately, Kapp & Stearn (1975) were unable to confirm the presence of this species and have suggested it to be a very rare species or 'an abnormal representative of *Labechia prima*'.

A stratigraphic break in the record of deposits and hence a gap in the course of evolutionary development occurs between the top of the Chazy Group and the base of the overlying Black River Group. According to Kapp & Stearn (1975) the basal formation of the Black River Group is the Pamela Formation and it contains the problematical cylindrical stromatoporoid *Cryptophragmus*. The succeeding Lowville and Leray Formations have a new stromatoporoid fauna apparently dominated by *Stromatocerium rugosum*. In addition to *Cryptophragmus* and *Stromatocerium*, Galloway & St. Jean (1961) have noted the first appearance of *Rosenella* and the enigmatic encrusting stromatoporoid *Dermatostroma* Parks 1910 in horizons of 'Blackriver' age. With the exception of *Cryptophragmus* most of the labechiid genera seem to range at least to the top of the Ordovician. *Cryptophragmus* however is confined to the North American late Middle Ordovician (i.e., 'Blackriver' and possibly 'Trenton').

The large, unbranched, cylindrical stromatoporoid *Aulacera* Plummer is characteristic of Richmond (Late Ordovician) horizons of North America (Galloway & St. Jean 1961). Also *Clathrodiction* has been reported by Twenhofel (1927, p. 107) from a similar level in the succession of Anticosti Island. The species recently figured by Copper (1974, p. 378) from a bioherm of the Ellis Bay Formation (late Richmond) on Anticosti seems to be the same species of *Clathrodiction* as Dr T. E.

Bolton of the Canadian Geological Survey (pers. comm.) has shown me from Member 6 of this formation. It is a representative of the *Clathrodictyon boreale* group of Nestor (1964). Workum, Bolton & Barnes (1976) have also recorded *Labechia*, *Cystostroma*? and *Aulacera* from the Ordovician succession of Akpatok Island, north-east Canada.

(c) *Europe*

The oldest stromatoporoid in European successions appears to be *Labechia aldonensis* Webby 1977 from the Stinchar Limestone of the Girvan district of Scotland. It occurs in an horizon of approximately middle-late Llandeilo age (Williams, 1962; Williams *et al.*, 1972).

On the island of Helgøya in the Nes-Hamar district of Norway, Størmer (1953) recorded the presence of a spectacular 'stromatoporoid reef' some 9-10 m thick in the Mjøsa Limestone. The Mjøsa Limestone is correlated with the Upper Chasmops Limestone (stage 4bd) of Oslo, or in terms of Estonian subdivisions, equivalent to the Oandu (D_{III}) or Rakvere (E) stages (middle-late Caradoc). As noted by Skjeseth (1963) the core of the reef near the shore of Lake Mjøsa consists of a massive framework of stromatoporoids. Sampling of the Mjøsa Limestone in the vicinity of Bergvika on the island of Helgøya has produced a varied stromatoporoid fauna with a few individual coenostea attaining dimensions of up to 1.3 m across and 0.4 m in height. The fauna includes representatives of *Labechia*, *Pachystylostroma* and a new genus allied to *Stromatocerium* (Webby, in press a). To the south the Encrinite Limestone of similar age to the Mjøsa Limestone also contains stromatoporoids.

Kaljo, Klaamann & Nestor (1963) have recorded two stromatoporoids from the Ashgill of Norway — *Clathrodictyon microundulatum* Nestor from stage 5a, and *Pachystylostroma* sp. nov. ex gr. *fragosa* Nestor from stage 5b. These elements correspond quite closely to faunas of the Pirgu (F_{Ic}) and Porkuni (F_{II}) stages of Estonia.

The Estonian Ordovician stromatoporoid succession has been fully described and analysed by Nestor (1964; 1966b). As outlined by him (1966b) the vesicular labechiids (*Stromatocerium*, *Cystostroma* and *Plumatalinia*) are typical of the period, but begin to be replaced by 'vesicular-laminar' clathrodictyids (*Clathrodictyon* and *Ecclimadictyon*) by Ashgill times. Two species of *Stromatocerium* are the first to appear in the Oandu (D_{III}) stage of middle-late Caradoc age. No stromatoporoids have been recorded from the succeeding Rakvere (E) and Nabala (F_{Ia}) stages, but the first clathrodictyids, *C. microundulatum* and *C. vormsiense* appear in the next stage, the Vormsi (F_{Ib}), about early-middle Ashgill time. The succeeding Pirgu (F_{Ic}) stage contains *Stromatocerium*, *Cystostroma* and *Plumatalinia* in addition to *C. microundulatum*. The topmost stage of the Ordovician in Estonia, the Porkuni (F_{II}), is characterized by new species of *Clathrodictyon*, *C. gregale*, *C. mammillatum* and *C. zonatum*, by the first *Ecclimadictyon* (*E. koigiense* and *E. porkuni*) and by *Pachystylostroma fragosum*.

On the western slope of the Urals, Bogoyavlenskaya (1973) has described an Ordovician stromatoporoid fauna comprising *Cystostroma concinnum* (Ivanov), *Stromatocerium definitum* (Ivanov), *Clathrodictyon microundulatum* Nestor and *Ecclimadictyon geniculatum* Bogoyavlenskaya. The species come from two horizons — the Typyl (topmost Middle Ordovician) and Rassokha (Late Ordovician, about the level of the zone of *Pleurogr. linearis*). The species of *Ecclimadictyon* is unusual in occurring in the older Middle Ordovician (Typyl) horizon (approximately equivalent to the level of *Dicranogr. clingani*, or to the Oandu stage, D_{III}, of Estonia; Whittington & Williams, 1964).

(d) *Asia*

In the Moiero River section in the northern part of the Siberian Platform, Nestor (1976) has recorded a succession of Middle-Late Ordovician stromatoporoid faunas. All are labechiids, and the oldest is *Cystostroma insuetum* Nestor from the Krivoluk stage of possible 'Blackriver' (Nestor 1976, p. 9) or ?Chazy (Sokolov *et al.*, 1960 p. 49) age. *Stromatocerium* cf. *sakuense* Nestor 1964 occurs in an higher, Middle Ordovician (? 'Trenton') horizon, and a much larger fauna appears in the Late Ordovician Dolbor stage. This latter fauna comprises *Cystostroma evenkiense* Nestor 1976, *Stromatocerium australe* Parks 1910, *S. pergratum* Nestor 1976, *Lophiostroma* sp. and *Pachystylostroma?* *amzassensis* (Khalfina 1960) — see earlier discussion p. 96. *Aulacera tenuipunctata* (Yavorsky 1955) occurs in still higher beds near the top of the Ordovician. Another form, reported by Yavorsky (1955) from the Late Ordovician of the Siberian Platform (Stony Tunguska and Moiero Rivers), is *Labechiella regularis* (Yabe & Sugiyama).

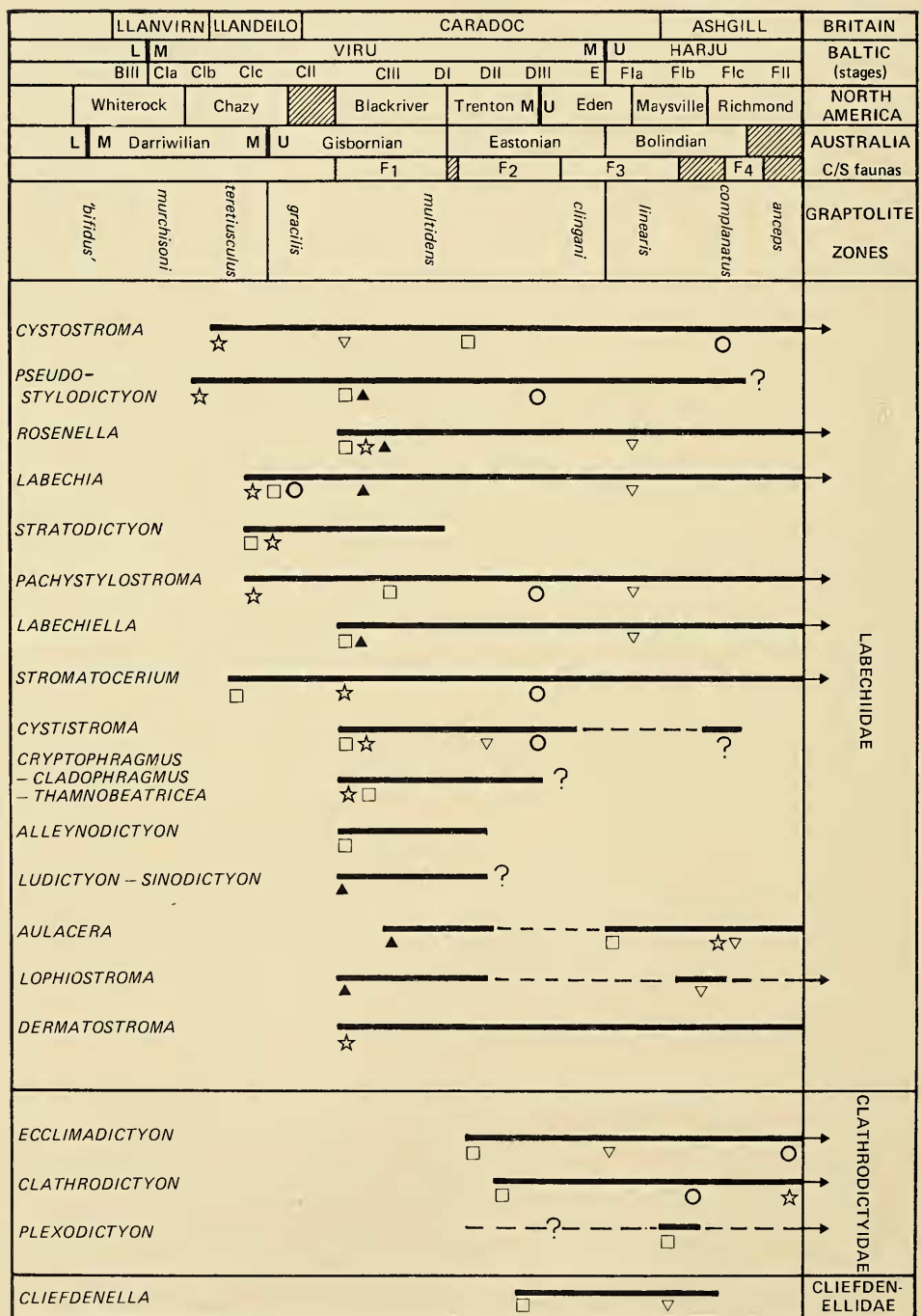
In the folded zone of the Altai Sayan mountain region of south-west Siberia there are many isolated records of Ordovician stromatoporoids. Khalfina (1960a) has described *Labechiella lophiostromoides* (Khalfina), *L. elandienne* (Khalfina), *Pachystylostroma?* *amzassensis* (Khalfina) and *Ecclimadictyon amzassensis* (Khalfina) from the upper part of the Amzass Formation (Late Ordovician) of Gornaya Shoriya and from similar levels in Gorny Altai. In approximate terms, the upper part of the Amzass Formation correlates with the zone of *Pleurogr. linearis* (Sokolov *et al.*, 1960). Khalfina & Yavorsky (1974) recorded *Cliefdenella permirum* from the Late Ordovician of Salair, and Bogoyavlenskaya (1971) referred to the presence of *Cystostroma* in the Middle and Late Ordovician of Tuva, and *Labechiella regularis* (Yabe & Sugiyama) and *Labechia huronensis* (Billings) from Late Ordovician horizons.

From the Late Ordovician Dulankara horizon in Kazakhstan, Khalfina (1958) has described (without illustration) *Labechiella kasachstanica*, and from the Late Ordovician of the Chatkal Range of Kirgizia, Middle Asia, Yavorsky (1961) has recorded *Cystostroma sarytschelekense*.

Another species of *Cystostroma*, *C. rarum* Yavorsky, of uncertain validity because of its intergrowth with *Labechia mirabilis* Yavorsky, is described by Yavorsky (1961) from the Late Ordovician of the Kolyma Basin of the north-eastern U.S.S.R.

In addition, many species of *Aulacera* have been described from Late Ordovician horizons from various parts of the Soviet Union by Yavorsky (1955; 1957; 1963), in particular from the Urals, from Novaya Zemlya, from the Vilyuy and Stony Tunguska Rivers of the Siberian Platform, and from eastern Siberia. A species of *Cryptophragmus*, *C. gracilis* is also recorded from the Ordovician of eastern Siberia by Yavorsky (1955).

Ordovician stromatoporoids have been reported from a number of regions of Eastern Asia — Shantung, Shansi and Liaotung (Southern Manchuria) provinces of North China, and North Korea (Yabe & Sugiyama 1930; Endo 1932; Ozaki 1938; Sugiyama 1941; Yang & Dong 1962). These occurrences all fall within the geographical limits of the major Hwangho Basin, and come from horizons of the Toufangian Series (and equivalents) of 'Middle' Ordovician (post Llandeilo and pre-Ashgill) age. Kobayashi (1969) has noted that stromatoporoids are the third largest fossil group in the Toufangian fauna of the Hwangho Basin, more specifically they occur mostly in horizons of the Toufangkou Limestone and the Ssuyen Formation (i.e., in the middle or upper parts of the Toufangian Series). There is no evidence of a faunal succession — merely an abundance of elements through a relatively restricted stratigraphical range, probably equivalent to the 'Blackriver', and possibly the



☆ NORTH AMERICA ▽ U.S.S.R. (EXCL. ESTONIA) ▲ CHINA □ AUSTRALIA ○ EUROPE (BRITAIN & BALTIC INCL. ESTONIA)

'Trenton' as well. The varied fauna includes records of some thirteen species from Shantung, nine from Liaotung, two from Shansi and two from North Korea. The genera include *Pseudostylodictyon*, *Labechia*, *Labechiella*, *Lophiostroma*, *Rosenella*, *Sinodictyon*, *Ludictyon* and *Aulacera*. The species of *Aulacera*, *A. peichuangensis* Ozaki, possibly represents the earliest record of the genus, earlier than the 'Eden-Maysville' appearances of the genus in Tasmania (Fig. 8). The association of *Aulacera* with other cylindrical forms (*Sinodictyon* and *Ludictyon*) may imply an evolutionary connection, with the Chinese fasciculate, branching 'Middle' Ordovician forms ancestral to the unbranched *Aulacera* (Fig. 10).

(e) *General significance*

The Ordovician labechiids exhibit a strikingly rapid period of diversification through the interval from the Llandeilo to the early Caradoc (from Chazy to 'Blackriver' using North American terminology, see Fig. 8). The earliest (Chazy) stocks, judging from Australian and North American first appearances, include *Pseudostylodictyon* (N. Amer.), *Cystostroma* (N. Amer. & ?Aust.), *Labechia* (N. Amer. & Aust.), *Stromatocerium* (Aust.), *Stratodictyon* (Aust.) and *Pachystylodictyon* (N. Amer.). They are followed by appearance of *Rosenella* (Aust.), *Labechiella* (Aust.), *Cystistroma* (Aust.), *Dermatostroma* (N. Amer.) and the first cylindrical forms — *Cryptophragmus* (N. Amer.) and *Alleynodictyon* (Aust.) — in the early Caradoc ('Blackriver') and correlatives (see Fig. 8).

With the records of *Lophiostroma*, *Sinodictyon*, *Ludictyon* and *Aulacera* in the 'Middle Ordovician' of China — possibly from equivalent 'Blackriver' (or ? 'Trenton') levels — it seems that the maximum period of generic diversification of labechiids from basic Chazy stocks occurred early in the history of the group. They maintained their presence as the major stromatoporoid group through the Middle and Late Ordovician (from 'Blackriver' to Richmond times) but declined in importance from the Silurian onwards. Less than half the Ordovician genera of labechiids (and none of the cylindrical forms) survived beyond the end of the Ordovician (Fig. 8). *Aulacera* whose cylindrical columns attained very large dimensions (5 m in height?) in beds of the latest Ordovician was perhaps the most spectacular form to become extinct.

From the apparent band-like spread of occurrences (Fig. 9), it appears that the Ordovician labechiids had approximately an equatorial distribution, perhaps limited to within 20° either side of the palaeoequator. The Middle Ordovician stocks seem to have a more restricted geographical spread — confined to eastern North America, Scotland, China and S.E. Australia — than the Late Ordovician forms (Fig. 9).

Despite the inadequacies of the preserved fossil record and the unevenness in the reliability of available data, it may be suggested that some of the labechiid elements like *Labechia* and *Cystostroma* seem to have achieved an 'equatorial' distribution during the Chazy, while others — *Pseudostylodictyon*, *Pachystylodictyon*, *Stromatocerium* and *Aulacera* — seem to have migrated very slowly to adjoining regions (Fig. 9). Others again appear to represent endemic elements, for instance, the

Fig. 8. Chart showing the known stratigraphic ranges of Ordovician stromatoporoid genera. The first appearance of each genus is shown by symbols for each major region. Those genera known to survive beyond the end of the Ordovician are depicted with arrows at the top of their Ordovician ranges. Correlations between the respective British, Baltic, North American and Australian stratigraphic subdivisions are only tentative. However, it should be noted that the boundaries between the Lower and Middle Ordovician, and between the Middle and Upper Ordovician, as shown in the columns by symbols L, M and U, occur at different levels in the respective Baltic, North American and Australian successions. C/S faunas — coral/stromatoporoids faunas of Webby (1969) and Webby & Morris (1976).

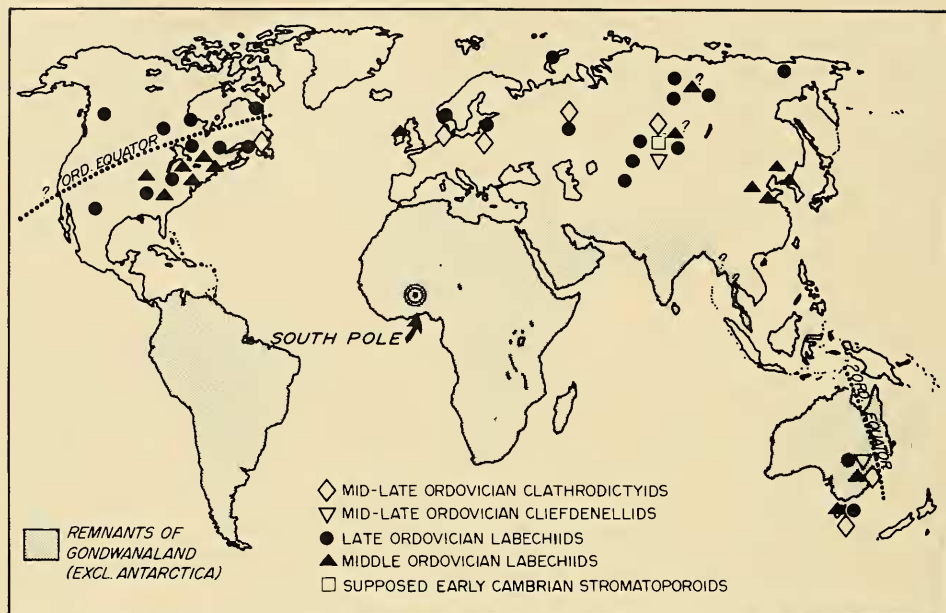


Fig. 9. Map illustrating the world-wide spread of Ordovician stromatoporoid faunas. Note also the single occurrence of the supposed Cambrian 'stromatoporoids' from the Altai Sayan mountain region of Siberia. Ordovician equatorial positions based on suggestions by Webby (1978) for Australia and Ross (1976) for North America.

problematical, encrusting *Dermatostroma* of North America, cylindrical *Sinodictyon* and *Ludictyon* of China, and cylindrical *Alleynodictyon* of Australia.

The clathrodictyid genera *Clathrodictyon* and *Ecclimadictyon* also exhibit patterns of slow global migration like a number of the labechiid genera. The genus *Clathrodictyon* which first appears in 'Trenton' correlatives in New South Wales, Australia, took until the Maysville (early Ashgill) to reach Estonia, and until the late Richmond to make its first appearance in North America, on Anticosti Island.

ORIGINS AND INTERRELATIONSHIPS

(a) *Supposed Cambrian 'Stromatoporoids'*

Although most workers have claimed the Middle Ordovician 'vesicular' labechiids to be the earliest representatives of the Stromatoporoidea with *Cystostroma* (Galloway, 1957; Galloway & St. Jean, 1961; Nestor, 1964; 1966a; Bogoyavlenskaya, 1969) or *Pseudostylodictyon* (Kapp & Stearn, 1975) seen to be ancestral to all later forms, a small group of Soviet specialists, notably Yavorsky (1932; 1940; 1947), Khalfina (1960a; 1960b; 1971), Vlasov (1961) and Khalfina & Yavorsky (1967; 1974), have maintained that the Ordovician stromatoporoids were derived from earlier, Cambrian stocks. The supposed stromatoporoid fauna occurs exclusively in the Early Cambrian of the Altai Sayan mountain region of south-west Siberia (Fig. 9). The fauna includes representatives of exclusively Cambrian genera (*Altaicyathus* Vologdin 1932; *Korovinella* Khalfina 1960b; *Praeactinostroma* Khalfina 1960b; *Cambrostroma* Vlasov, 1961), and others which may be linked with established post-

Cambrian forms — the genera *Clathrodictyon* Nicholson & Murie 1878, *Rosenellina* Radugin 1936 and *Stromatocerium* Hall 1847.

Korovinella (type species *Clathrodictyon sajanicum* Yavorsky) is the best known genus, typically exhibiting porous laminae, short, rod-like pillars, and vertical canals, the latter possibly analogous to the astrorhizal columns of stromatoporoids (Khalfina 1960a; 1960b). The porous nature of the laminae, on the other hand, is noted by Nestor (1966a) to ally the genus to archaeocyathans. *Praeactinostroma* (type species *Actinostroma vologdini* Yavorsky) has both discontinuous rod-like horizontal elements and pillars forming an incomplete, reticulate network also intersected by vertical canals. It appears to have closer affinities to stromatoporoids by resembling the Silurian genus *Plectostroma* Nestor 1964 and Mesozoic genus *Actinostromaria* Chalmers in Dehorne 1920 (see Nestor 1966a). Of the other forms, Nestor (1966a) has viewed *Cambrostroma* as a junior synonym of *Korovinella*, he has noted that Radugin's Cambrian species of *Rosenellina* has never been described and cannot be discussed further, and he has observed that Vlasov's species of *Clathrodictyon* (*C. formozovae*) is based on such small fragments that they cannot be satisfactorily revised.

Altaicyathus (type species *A. notabilis*) was originally described as an archaeocyathan by Vologdin (1932), but it was later included by Yavorsky (1940), Zhuravleva (1955; 1960), Khalfina (1960b) and Vologdin (1966) in stromatoporoids. *Korovinella* Khalfina 1960b has been regarded by Vlasov (1967) as a junior synonym of *Altaicyathus* Vologdin 1932 (see also Hill, 1972, p. E142, and Flügel & Flügel-Kahler, 1968, p. 525), so perhaps both *Korovinella* and *Cambrostroma* should be included in *Altaicyathus*. However at least one species of *Korovinella*, *K. edelsteini* (Yavorsky), has recently been equated with the archaeocyathan *Abakanicyathus karokolensis* Konjuschkov — see Zhuravleva & Miagkova (1974, pl. 2, fig. 2).

Two species of *Stromatocerium*, *S. pospelovi* Khalfina in Khalfina & Yavorsky 1974 and *S. cambricum* Khalfina in Khalfina & Yavorsky 1974 are recorded as coming from the Cambrian of the Kuznetsky Alatau, south-west Siberia. With their meandriiform pillar structures, the species seem to have more in common with forms from the Early Carboniferous of China — like *Stromatocerium kwangsiense* Dong 1964 — than with typical Ordovician species of the genus (Parks, 1910; Galloway & St. Jean, 1961).

Galloway (1957) noted that the supposed Cambrian stromatoporoids of Yavorsky (1932) were not composed of simple cysts as would be expected if they were ancestral to *Cystostroma* and *Pseudostylodictyon* but included more complex structures with laminae, pillars and astrorhizae. He implied (see also Galloway & St. Jean, 1961, p. 7) that the forms were collected from younger horizons than the Cambrian. Galloway also thought that the stromatoporoids as a group may have evolved from the archaeocyathans, from a form like *Exocyathus* Bedford & Bedford, but did not, in view of his doubts about the stratigraphic position of Yavorsky's finds, explore the possibility of the supposed Cambrian forms being transitional between archaeocyathans and stromatoporoids. The more recent work of Yavorsky, Khalfina and Vlasov has proved beyond doubt that the bulk of the forms come from the Early Cambrian of the Altai-Sayan mountain region; typically they have an association with archaeocyathans, even within the one specimen.

Nestor (1966a) interpreted the supposed Cambrian stromatoporoids (excluding the recently reported species of *Stromatocerium*) as archaeocyathans being only convergently similar to stromatoporoids. According to him, the forms disappeared from the stratigraphic record towards the end of the Early Cambrian and had no

successors in the Middle-Late Cambrian or the Early Ordovician. He argued against them being the ancestors of the Middle Ordovician stromatoporoids, the earliest being the 'vesicular' labechiids. On the other hand, archaeocyathan specialists such as Vologdin (1966) and Hill (1972) have excluded the supposed Cambrian 'stromatoporoids' from a grouping with archaeocyathans.

Khalfina & Yavorsky (1967) in reply to Nestor reiterated that the Cambrian forms were the oldest stromatoporoids, and that they were morphologically distinct from archaeocyathans. They noted that vertical canals were shown to be arranged like the astrorhizal canals of stromatoporoids, and the external and internal walls of typical archaeocyathans were lacking. The coniform-cylindrical 'coenostea' of forms like *Korovinella* and *Praeactinostroma* were seen to bear similarities to cylindrical coenostea of some later Palaeozoic (post Ordovician) stromatoporoids, for example, in exhibiting similar patterns of laminae arranged transversely to the axial canal (*Paramphipora*), lateral processes (*Idiostroma*, *Stachyodes*) and a single axial canal (*Amphipora*, *Idiostroma*). The genus *Clathrodictyon* was seen by Khalfina & Yavorsky to be unrelated to 'vesicular' stromatoporoids, and possibly to have been derived from Cambrian 'stromatoporoids' with perforate laminae. The porous nature of the laminae in *Korovinella* was regarded as being different from the arrangement of pores in tabulae of irregular archaeocyathans (Suborder Archaeosyconina), and the mode of lamina formation in *Korovinella* similar to that of stromatoporoids like *Actinostroma* (another post Ordovician form). I question these latter assertions. First, the perforate laminae of *Korovinella* closely resemble the porous tabulae of irregular archaeocyathans like *Hupecyathus* Debrenne 1964. Secondly, the perforate laminae of *Korovinella* differ markedly from the laminae of *Actinostroma* (composed of an hexactinellid network of radial processes — see Stearn, 1966, p. 86).

Zhuravleva (1970) has noted that the skeletal structures of archaeocyathans of the class Irregulares with 'colonial' form may be practically indistinguishable from stromatoporoids like *Clathrodictyon* (Zhuravleva & Miagkova, 1974). The tabulae, vertical rods and central cavities of irregular archaeocyathans are recognized as having equivalents in the laminae, pillars and astrorhizae of stromatoporoids. Zhuravleva & Miagkova (1974) have emphasized the morphological similarities between stromatoporoid *Amphipora* and irregular archaeocyathan *Protopharetra*, and between *Korovinella* and *Archaeosycon*. They have additionally shown the supposed Cambrian 'stromatoporoids' *Korovinella edelsteini* and *Praeactinostroma* to be indistinguishable from irregular archaeocyathans *Abakanicyathus karakolensis* Konjuschkov and *Claruscyathus cumfundus* (Vologdin), respectively (Zhuravleva & Miagkova, 1974, pl. 2).

In terms of presently accepted views of morphology and classification of stromatoporoids the Cambrian 'stromatoporoid' genera of Yavorsky, Khalfina and Vlasov include three (possibly four) stocks, each of which may be grouped in a different family. *Altaicyathus* (= *Korovinella*) belongs to the exclusively Cambrian family Korovinellidae Khalfina 1960b, *Praeactinostroma* should probably be included in the family Actinostromatidae Nicholson 1886 (a group which has no confirmed Ordovician record) and *Clathrodictyon* is a member of the Clathrodictyidae. A possible fourth is the presumed *Stromatocerium* (family Labechiidae). The korovinellids are the best known group but have the least close resemblances to Middle Ordovician or later stromatoporoids. *Praeactinostroma* bears no close relationships to Middle-Late Ordovician stromatoporoids. *Clathrodictyon* and *Stromatocerium* remain too inadequately documented. *Clathrodictyon* is based on totally insufficient material and *Stromatocerium* has yet to be confirmed as coming from undoubted Cambrian horizons. Their essentially localized occurrence with archaeocyathans in the

Altai Sayan mountain region of Siberia and morphological resemblances with members of the class Irregulares, and their physical separation by such an enormous break in continuity of record of some 110 m.y. from Middle Ordovician stromatoporoids, make it impossible to establish them as the earliest, indubitable stromatoporoids. The occurrences of *Clathrodictyon* and *Stromatocerium* may represent the earliest records of clathrodictyids and labechiids, respectively, but they may equally well be viewed as homeomorphs of later stromatoporoids (either offshoots of irregular archaeocyathans, or members of an independent group). There is no record of such structures after the extinction of the reef-forming archaeocyathans at the end of the Early Cambrian, until the Middle Ordovician when skeletal reef habitats reappeared.

(b) *Outline of Evolutionary Development of Ordovician Stromatoporoids*

The Middle Ordovician stromatoporoids formed an important 'skeletonized' constituent of the earliest 'coral-stromatoporoid-algal' reef communities (Pitcher, 1971; Heckel, 1974; Copper, 1974; Kapp, 1975). Their skeletal remains were among the more prominent components of Middle-Late Ordovician patch reef and carbonate bank deposits. The advent of skeletonization may have represented an adaptive breakthrough allowing for a dramatic increase in size (some Chazy stromatoporoids are up to 1 m in width and height), providing the necessary support for the mantling soft tissues, and elevating the individuals above the substrate to facilitate their filter feeding (Stearn, 1972), epifaunal mode of life. The sessile stromatoporoid animal evidently lived in a moderately competitive, near-equatorial, shallow-water patch reef or carbonate bank-type environment.

The main burst of adaptive radiation of the labechiids occurred in the Middle Ordovician, seemingly with the genera derived from a *Cystostroma* or *Pseudostylodictyon*-like ancestor, as shown in Fig. 10. From the nature of the radiation of skeletonized genera (Figs. 8, 10), it appears that we are viewing a genuine invasion of patch reef and bank habitats previously relatively free from competitors. The early appearance of *Stromatocerium* from the Tasmanian 'Middle Ordovician' (Fig. 8), an 'advanced' form in terms of its occurrence at the end of an evolutionary pathway (see *Stromatocerium* group B in Fig. 10) may merely serve to indicate how rapidly the adaptive radiation took place in the Chazy, rather than to suggest links with a supposed Early Cambrian *Stromatocerium* archetype (Khalfina & Yavorsky, 1974).

Recognition in some labechiids of immature and mature (or alternating) growth stages — the basal layers of coenostea (and the bases of latilaminae) exhibiting immature stages of growth — may be significant in clarifying phylogenetic relationships within the group (Galloway, 1957). For example, Galloway (1957, p. 394) noted in one specimen of *Cystistroma canadensis* the presence of a *Rosenella*-type 'immature' stage, and Kapp & Stearn (1975) have observed *Cystostroma* as the 'immature' stage of *Labechia prima*.

Morphologically the most simple, calcified laminar hemispherical forms are *Cystostroma*, *Pseudostylodictyon* and *Rosenella* (Fig. 10). They typically exhibit rows of simple cysts (or laminae in *Pseudostylodictyon*) arranged in an imbricated manner, denticles on their upper surfaces and mamelons but no pillars. By simple superposition of denticles to form rounded pillars, the genera *Labechia* (*L. prima* group), *Stratodictyon* and *Pachystylostroma* may be derived. In view of the growth stages exhibited by *Labechia* (Yavorsky, 1961; Kapp & Stearn, 1975) *Cystostroma*, rather than *Pseudostylodictyon*, should be regarded as its ancestor. *Stratodictyon* appears to have been derived from a member of the *L. prima* group, or less likely, directly from

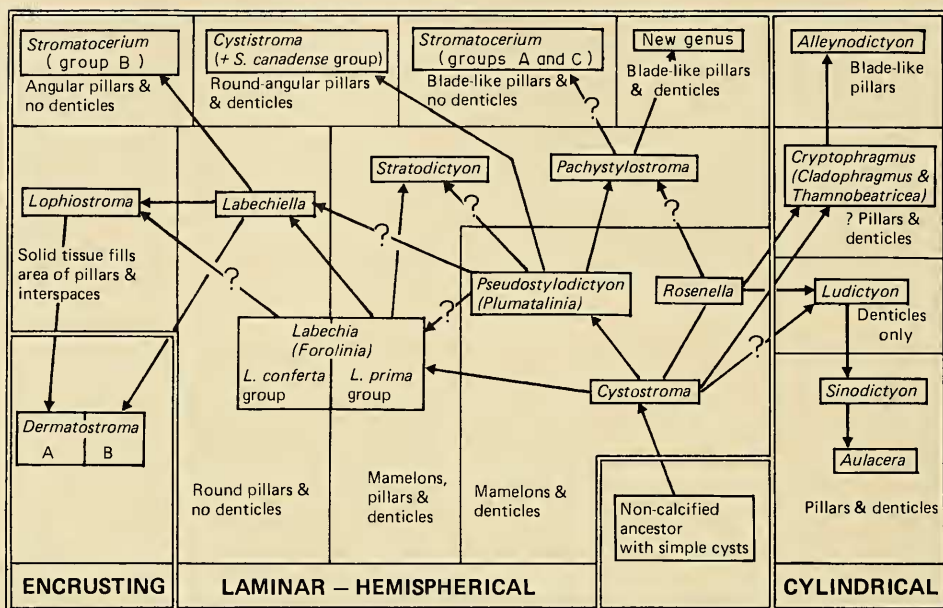


Fig. 10. Diagram showing possible evolutionary pathways for the Ordovician genera of labechiid stromatoporoids.

Pseudostylocidictyon (Webby, 1969, p. 653), while *Pachystylostroma* appears to have evolved, as Kapp & Stearn (1975) have outlined, from *Pseudostylocidictyon*. The culmination of the trend towards long and continuous pillars derived from superposed denticles leads to representatives of *Labechia* (*L. conferta* group) with cysts and *Labechiella* with laminae. *Stromatocerium* (*S. rugosum* group) is derived from *Labechiella* and has irregular (secondarily altered) pillars. None of these latter forms exhibits denticles.

Derivation of *Lophiostroma* and *Dermatostroma* is more problematical. The clue to the derivation of *Lophiostroma* with its poorly differentiated internal structures owing to a completely solid infill of tissue is seen in the Middle Ordovician species *L. shantungensis* which shows traces of original pillars and a few large unfilled cysts in the interspaces, as in a *Labechiella* or *Labechia*. Furthermore the upper surface of the coenosteum of the respective type species of *Lophiostroma* and *Labechia* have an identical papillose appearance. The encrusting genus *Dermatostroma* includes forms with solidly fused vertically aligned prisms which may be allied to *Lophiostroma* (*Dermatostroma* A in Fig. 10), and forms with a few laminae and pillars which may be related to *Labechiella* (*Dermatostroma* B in Fig. 10).

Cystistroma, as previously suggested by Webby (1969, p. 653), may have been derived from *Pseudostylocidictyon* with the large, rounded-angular pillars evolving from mamelons, not from denticles. The new *Stromatocerium*-like genus (Webby, in press a) bears similarities to *Cystistroma* in exhibiting denticles on upper surfaces of cysts in the interspaces between the large pillars but differs in having 'composite' vane-like pillars, each apparently developed at the site of a former mamelon. It seems to have a different derivation from *Cystistroma*, probably from a *Pachystylostroma*. Other forms with large 'hollow' wall-like radiating pillars of *S. rugosum* type (group A of Fig. 10) and slender, intermeshed, 'composite' blade-like pillars, referred to the

Stromatocerium michiganense group (group C of Fig. 10) may have a similar origin, but they lack denticles.

The cylindrical labechiids appear to have evolved from the laminar-hemispherical forms by the development of extended mamelon-like upgrowths perhaps from a *Cystostroma*-like base (Galloway & St. Jean, 1961). The relationships have not been clearly established but there would appear to be two main trends (Fig. 10) — one through the Chinese fasciculate-cylindrical genera *Ludictyon* and *Sinodictyon* to the large unbranched *Aulacera*, and the other through the slender North American forms of *Cryptophragmus*, *Cladophragmus* and *Thamnobeatricea* to *Alleynodictyon*, a genus with blade-like pillars (Webby, 1971). Both lines would appear to commence with a simple *Rosenella* or *Cystostroma*-like ancestor.

Clathrodictyids may have been derived from a simple labechiid ancestor, but evolved pillars from downward inflections of laminae rather than by superposition of denticles as in labechiids, and developed walled astrorhizae. Adequate time seems to have been available for these morphological changes to have taken place, given a line of descent from a Chazy, *Cystostroma*-like ancestor to the first appearance of clathrodictyids in the 'Trenton' (Fig. 8). The alternative is a much earlier, independent ancestry for the group, possibly from the Early Cambrian *Clathrodictyon* of Vlasov (1961) and Khalfina & Yavorsky (1967). To be directly ancestral to Middle Ordovician and later representatives of the genus would imply that the supposed Early Cambrian *Clathrodictyon* lost its ability to preserve a mineralized skeleton for a period of 110 m.y. to the Middle Ordovician.

It is more difficult to derive the complex morphology of the cliefdenellids from a labechiid. The group may have evolved from a clathrodictyid like *Plexodictyon* but there would seem to be too limited a period of time within the 'Trenton' (Fig. 8) to make all the necessary morphological changes, viz., addition of denticles to the upper surface of its primary laminae, large tube-like pillars and complex astrorhizae. A more realistic view allowing for the development of the complex morphological features is to suggest that cliefdenellids arose as an independent Ordovician group from an earlier, possibly Cambrian soft-bodied ancestor.

The marked morphological differences between the three separate families of Ordovician stromatoporoids favour a much earlier origin possibly from a common (? soft-bodied) ancestor in the Cambrian (very doubtfully from within the irregular archaeocyathans, suborder Archaeosyconina), with independent lines of descent through the Ordovician. The initial Middle Ordovician record of each family is based on the appearance of its first skeletonized remains, and does not necessarily coincide with the origins of the individual group.

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References

- ALLOITEAU, J., 1952. — Classe des Hydrozoaires. In Piveteau, J. (ed.), *Traité de Paléontologie*, I: 377-398. Masson & Cie, Paris.
- BANKS, M. R., 1962. — Ordovician System. In Spry, A. & Banks, M. R. (eds). *The geology of Tasmania*. *J. geol. Soc. Aust.*, 9: 147-176.

- BILLINGS, E., 1857. — Ordovician and Silurian rocks of North America. *Geol. Surv. Canada, Rept. Progress, 1853-1856*: 343-345.
- BIRKHEAD, P. K., 1967. — Stromatoporoidea of Missouri. *Bull. Amer. Paleont.*, 52: 21-110.
- BOGOYAVLENSKAYA, O. V., 1969. — K. postroyeniye klassifikatsii stromatoporoidey. *Paleont. Zhurn.*, 1969, 4: 12-27.
- , 1971. — Ordovikiyskiye i siluriyskiye labekhiidy Tuvy. *Paleont. Zhurn.*, 1971, 3: 32-38.
- , 1973. — Ordovikiyskiye stromatoporoidei zapadnogo sklona Urala. *Paleont. Zhurn.*, 1973, 4: 18-24.
- , 1974. — Principy sistemizatsii stromatoporoidey. In Sokolov, B.S. (ed.). *Drevniye Cnidaria*, I: 20-27. Nauka, Novosibirsk.
- BOLSHAKOVA, L. N., 1973. — Stromatoporoidei silura i nizhnego devona podolii. *Trudy Paleont. Inst. Akad. nauk SSSR*, 141: 1-136.
- BOLTON, T., 1972. — Geological map and notes on the Ordovician and Silurian litho- and biostratigraphy, Anticosti Island, Quebec. *Pap. geol. Surv. Can.*, 71: 19-44.
- COPPER, P., 1974. — Structure and development of early Palaeozoic reefs. *Proc. Second Int. Coral Reef Symp.*, 1: 365-386. Brisbane.
- CORBETT, K. D., and BANKS, M. R., 1973. — Ordovician stratigraphy of the Florentine Synclinorium, southwest Tasmania. *Pap. Proc. R. Soc. Tasm.*, 107: 207-238.
- DEBRENNÉ, F., 1964. — Archaeocyatha. Contribution à l'étude des faunes cambriennes du Maroc, de Sardaigne et de France. *Serv. Mines Carte Géol. Maroc, Notes & Mém.*, 179 (1-2): 1-265.
- DEHORNE, Y., 1920. — Les stromatoporoïdes des terrains secondaires. *Mém. servir explic. carte géol. France*: 1-170.
- DONG, D. Y., 1964. — Stromatoporoïdes from the Early Carboniferous of Kwangsi and Kueichow. *Acta Palaeont. sinica*, 12 (2): 280-299.
- ENDO, R., 1932. — The Canadian and Ordovician formations and fossils of South Manchuria. *U.S. Nat. Mus. Bull.*, 164: 1-152.
- ETHERIDGE, R. JR., 1895. — On the occurrence of a stromatoporoid, allied to *Labechia* and *Rosenella*, in Siluro-Devonian rocks of N.S. Wales. *Rec. Geol. Surv. N.S.W.*, 4: 134-140.
- FLÜGEL, E., and FLÜGEL-KÄHLER, E., 1968. — Stromatoporoidea (Hydrozoa palaeozoica). In Westphal, F., (ed.). *Fossilium Catalogus I: Animalia*, pts 115-116: 1-681. 's-Gravenhage.
- GALLOWAY, J. J., 1957. — Structure and Classification of the Stromatoporoidea. *Bull. Amer. Paleont.*, 37 (164): 345-480.
- , and ST. JEAN, J., 1961. — Ordovician Stromatoporoidea of North America. *Bull. Amer. Paleont.*, 43 (194): 1-111.
- GORSKY, I. I., 1938. — Nekotorye Stromatoporoidea iz paleozoiskikh otlozhenii Novoi Zemli. *Trudy Arkt. Inst.*, 101: 7-45.
- HALL, J., 1847. — *Palaeontology of New York. Vol 1.* Containing descriptions of the organic remains of the lower division of the New York System. 339 pp. Nat. Hist. New York, Albany.
- HECKEL, P. H., 1974. — Carbonate buildups in the geologic record: a review. In Laporte, L. F. (ed.). *Reefs in Time and Space. Soc. Econ. Paleont. Min. Spec. Publ.* 18: 90-154.
- HEINRICH, M., 1914. — Über den Bau und das System der Stromatoporoidea. *Zentralbl. Min. Geol. Palaeont.*, B, 732-736.
- HILL, D., 1972. — Archaeocyatha. In Teichert C. (ed.). *Treatise on invertebrate paleontology*. Part E, Vol. 1, Second Edit. E1-158. Univ. of Kansas & Geol. Soc. Amer., Lawrence.
- KALJO, D., KLAAMANN, E., and NESTOR, H. A., 1963. — Nekotorye obschie cherty fauny korallov i stromatoporoidei ashgillya Estonii i Norvegii. *Trudy Inst. Geol. Akad. nauk. Est. SSR*, 13: 75-81.
- KAPP, U. S., 1974. — Mode of growth of middle Chazyan (Ordovician) stromatoporoïdes, Vermont. *J. Paleont.*, 48: 1235-1240.
- , 1975. Paleoecology of Middle Ordovician stromatoporoïd mounds in Vermont. *Lethaia*, 8: 195-207.
- , and STEARN, C. W., 1975. — Stromatoporoïdes of the Chazy Group (Middle Ordovician), Lake Champlain, Vermont and New York. *J. Paleont.*, 49: 163-186.
- KAŹMIERCZAK, J., 1971. — Morphogenesis and systematics of the Devonian Stromatoporoidea from the Holy Cross Mountains, Poland. *Palaeontol. Polonica*, 26: 1-150.
- , 1976. — Cyanophycean nature of stromatoporoïdes. *Nature*, 264: 49-51.
- KHALFINA, V. K., 1958. — O novom predstavitele podroda *Labechiella* Yabe & Sugiyama iz ordovika Kazakhstana. *Trudy geol. inst. Akad. nauk. SSSR*, 9: 229-232.
- , 1960a. — Stromatoporoidei. In Khalfin, L. L. (Ed.), *Biostratigrafiya paleozoya Sayono-Altayskoy Gornoy oblasti. Tom. I, Nizhniy Paleozoy. Trudy sib. nauchno-issled. Inst. Geol. Geofiz. miner. Syr.*, 19: 82-84, 141-143, 357-358, 370-373.
- , 1960b. — Stromatoporoidei iz kembriiskikh otlozhenii Sibiri. In Materialy po paleontologii i stratigrafii Zapado Sibiri. *Trudy sib. nauchno-issled. Inst. Geol. Geofiz. miner. Syr.*, 8: 79-83.
- , 1971. — Stromatoporoidei. In Sokolov, B. S.; Ivanovskiy, A. B., Krasnov, E. V. (eds), *Morfologiya i terminologiya kishechnopolostnykh. Trudy Inst. Geol. Geofiz. sib. otd.*, 133: 14-22.

- , and YAVORSKY, V. I., 1967. — O drevneishikh stromatoporoideyakh. *Paleont. Zhurn.*, 1967, 3: 133-136.
- , and —, 1973. — Klassifikatsiya stromatoporoidey. *Paleont. Zhurn.*, 1973, 2: 19-34.
- , and —, 1974. — K evolyutsii stromatoporoidey. In Sokolov, B. S. (ed.), *Drevniye Cnidaria*, I: 38-45. Nauka, Novosibirsk.
- KHROMYCH, V. G., 1974a. — Devonskiye stromatoporoidei severo-vostoka S.S.S.R. *Trudy Inst. Geol. Geofiz. sib. otd. Akad. nauk. SSSR*, 64: 1-104.
- , 1974b. — Filogeniya i istoricheskoe razvitiye nekotorykh rodov stromatoporoidey. In Sokolov, B. S. (ed.), *Drevniye Cnidaria*, I: 45-50. Nauka, Novosibirsk.
- KOBAYASHI, T., 1969. — The Ordovician of Eastern Asia and other parts of the Continent. *J. Fac. Sci (Imp.) Univ. Tokyo, Sect. II*, 17: 163-316.
- KÜHN, P., 1927. — Zur Systematik und Nomenklatur der Stromatoporen. *Zentralbl. Min. Geol. Paläont.*, B: 546-551.
- , 1939. — Hydrozoa. In Schindewolf, O. H., *Handbuch der Paläozoologie Bd. 2A*: 1-68. Borntraeger, Berlin.
- LECOMPTÉ, M., 1956. — Stromatoporoidea. In Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology. Part F*: 107-144. Geol. Soc. Amer. & Univ. Kansas Press, Lawrence.
- LONSDALE, W., 1839. — Corals. In Murchison, R. I. *The Silurian System*, part 2: 675-694. J. Murray, London.
- MCLEAN, R. A., and WEBBY, B. D., 1976. — Upper Ordovician rugose corals of central New South Wales. *Proc. Linn. Soc. N.S.W.*, 100: 231-244.
- MILNE-EDWARDS, H., and HAIME, J., 1851. — Monographie des Polypiers fossils des Terraines Paleozoïques, precedee d'un tableau general de la classification des Polypes. *Arch. Mus. Hist. natur.*, Paris, 5: 1-502.
- MORI, K., 1969. — Stromatoporoids from the Silurian of Gotland, Pt 2. *Stockh. Contr. Geol.*, 22: 1-152.
- NESTOR, H. A., 1960. — *Plumatalinia* — novyi rod otryada stromatoporoidea iz verkhnego ordovika estonskoi S.S.R. *Izvest. Akad. nauk. Est. SSR*, 9: 225-228.
- , 1962. — Reviziya stromatoporoidea, opisannykh F. Rozonom v 1867 gody. *Trudy Inst. Geol. Akad. nauk. Est. SSR*, 9: 3-23.
- , 1964. — Stromatoporoidei ordovika i llandovery Estonii. *Inst. Geol. Akad. nauk. Est. SSR*, Tallinn: 1-112.
- , 1966a. — O drevneishikh stromatoporoideyakh. *Paleont. Zhurn.*, 1966, 2: 3-12.
- , 1966b. — Stromatoporoidei wenlocka i ludlowa Estonii. *Inst. Geol. Akad. nauk. Est. SSR*, Tallinn: 1-87.
- , 1974. — O filogenii paleozoiskikh stromatoporoidey. In Sokolov, B. S. (ed.), *Drevniye Cnidaria*, I: 27-38. Nauka, Novosibirsk.
- , 1976. — Rannepaleozoiskie stromatoporoidei basseina reki Moiero (sever Sibirskoi platformi). *Inst. Geol. Akad. nauk. Est. SSR*, Tallinn: 1-95.
- NICHOLSON, H. A., 1879. — *On the Structure and Affinities of the Tabulate Corals of the Palaeozoic Period*. xii + 342 pp. Blackwood & Sons, Edinburgh & London.
- , 1886a. — A Monograph of the British Stromatoporoids, Part I. General Introduction. *Palaeontogr. Soc.*, [Monogr.]: 1-130.
- , 1886b. — On some New or Imperfectly-known Species of Stromatoporoids Part II. *Ann. Mag. Nat. Hist.*, (5) 18: 8-22.
- , 1891. — A Monograph of the British Stromatoporoids, Part III. Description of Species. *Palaeontogr. Soc.*, [Monogr.]: 159-202.
- , and MURIE, J., 1878. — On the minute structure of *Stromatopora* and its allies. *J. Linn. Soc., Zool.*, 14: 187-246.
- OZAKI, K. E., 1938. — On some stromatoporoids from the Ordovician limestone of Shantung and South Manchuria. *J. Shanghai Sci. Inst.*, Sect. 2, 2: 205-223.
- PARKS, W. A., 1910. — Ordovician stromatoporoids. *Univ. Toronto Stud., geol. ser.*, 7: 1-52.
- PITCHER, M., 1971. — Middle Ordovician reef assemblages. In Reef organisms through time. *Proc. North Amer. Paleont. Convention, Part J*: 1341-1357. Allen Press, Lawrence.
- PLUMMER, J. T., 1843. — Suburban geology, or rocks, soil and water about Richmond, Wayne County, Indiana. *Amer. J. Sci.*, 44: 281-313.
- RADUGIN, K. V., 1936. — Nekotorye Tselenteraty iz nishnego silura gornoi Shorii. *Materialy po Geologii zapadno-sibirskogo kraya*, 35: 89-106.
- RAYMOND, P. E., 1914. — A Beatricea-like organism from the Middle Ordovician. *Bull. Geol. Surv. Mus. Canada*, 5: 1-19.
- , 1931. — Notes on invertebrate fossils, with descriptions of new species. *Bull. Mus. Comp. Zool., Harvard*, 9: 165-312.
- ROSS, R. J. Jr, 1976. — Ordovician sedimentation in the Western United States. In Bassett, M. G. (ed.). *The Ordovician System*: 73-105. Univ. Wales Press and Nat. Mus. Wales, Cardiff.

- SCHMIDT, F., 1858. — Untersuchungen über die Silurische Formation von Esthland, Nord-Livland und Oesel. *Archiv F. naturk. Liv-, Esth- und Kurlands*, (1), 2: 1-248.
- SCHUCHERT, C., 1919. — The proper name for the fossil hydroid *Beatricea*. *Amer. J. Sci.*, 47: 293-296.
- SEELY, H. M., 1904. — The Stromatoceria of the Isle La Motte, Vermont. *Rep. State Geol. Vermont*, 4: 144-152.
- SKJESETH, S., 1963. — Contributions to the geology of the Mjøsa Districts and the classical sparagmite area in Southern Norway. *Norg. geol. Unders.*, 220.
- SLEUMER, B. H. G., 1969. — Devonian stromatoporoids of the Cantabrian Mountains (Spain). *Leidse geol. Meded.*, 44: 1-136.
- SOKOLOV, B. S., ALIKHOVA, T. N., KELLER, B. M., NIKIFOROVA, O. I., and OBUT, A. M., 1960. — Stratigraphy, correlation and paleogeography of the Ordovician deposits of the U.S.S.R. *Rept. 21st int. geol. Congr. Copenhagen*, Part VII: 44-57.
- ST. JEAN, J. JR., 1967. — Maculate tissue in Stromatoporoidea. *Micropaleont.*, 13 (4): 419-444.
- STEARN, C. W., 1966. — The microstructure of stromatoporoids. *Palaeontology*, 9: 74-124.
- , 1969. — The stromatoporoid genera *Tienodictyon*, *Intexodictyon*, *Hammatostroma* and *Plexodictyon*. *J. Paleont.*, 43: 753-766.
- , 1972. — The relationship of the stromatoporoids to the sclerosponges. *Lethaia*, 5: 369-388.
- , 1975. — The stromatoporoid animal. *Lethaia*, 8: 89-100.
- , and HUBERT, C., 1966. — Silurian stromatoporoids of the Matapedia Temiscouata area, Quebec. *Canad. J. Earth Sci.*, 3: 31-48.
- STØRMER, L., 1953. — The Middle Ordovician of the Oslo Region, Norway, No. I. Introduction to stratigraphy. *Norsk geol. Tidsskr.*, 31: 37-141.
- SUGIYAMA, T., 1939. — Geological and geographical distribution of stromatoporoids in Japan, with notes on some interesting forms. *Yabe Jubilee Publ.*, 1: 427-456.
- , 1940. — Stratigraphical and paleontological studies of the Gotlandian deposits of the Kitakami mountainland. *Sci. Repts Tōhoku Imp. Univ.*, ser. 2 (Geol.), 21 (2): 81-146.
- , 1941. — A new form of the genus *Labechiellata* from Tyosen (Korea). *J. geol. Soc. Japan*, 48: 461-463.
- SWEET, W. C., and BERGSTRÖM, S. M., 1976. — Conodont biostratigraphy of the middle and upper Ordovician of the United States Mid-continent. In Bassett, M. G. (ed.). *The Ordovician System*: 121-151. Univ. Wales Press and Nat. Mus. Wales, Cardiff.
- TRIPP, K., 1929. — Untersuchungen über den Skelettbau von Hydractinien zu einer vergleichenden Betrachtung der Stromatoporen. *N. Jb. Miner. Geol. Palaont.*, B, 62: 467-508.
- TWENHOFEL, W. H., 1927. — Geology of the Anticosti Island. *Geol. Surv. Can., Mem.*, 154: 1-481.
- VLASOV, A. N., 1961. — Kembriiskie stromatoporoidei. *Paleont. Zhurn.*, 1961, 3: 22-32.
- , 1967. — O rode *Altaicyathus* Vologdin. *Paleont. Zhurn.*, 1967, 1: 120.
- VOLOGDIN, A. G., 1932. — Arkheotsiaty Sibiri. 2. Fauna kembriiskikh izvestnyakov Altaya. *Izd. Gos. Geol. - razved. Uprav.*, 1-106. Moskva-Leningrad.
- , 1966. — Kribritsiaty kembriya S.S.S.R. *Trudy Paleont. Inst. Akad. nauk, SSSR*, 109: 1-62.
- WEBBY, B. D., 1969. — Ordovician stromatoporoids from New South Wales. *Palaeontology*, 12: 637-662.
- , 1971. — *Alleynodictyon*, a new Ordovician stromatoporoid from New South Wales. *Palaeontology*, 14: 10-15.
- , 1975. — Succession of Ordovician coral and stromatoporoid faunas from central-western New South Wales, Australia. In Sokolov, B. S. (ed.), *Drevniye Cnidaria*, II: 57-68. Nauka, Novosibirsk.
- , 1976. — The Ordovician System in South-eastern Australia. In Bassett, M. G. (ed.), *The Ordovician System*: 417-446. Univ. Wales Press and Nat. Mus. Wales, Cardiff.
- , 1977. — *Labechia aldonensis* sp. nov., an Ordovician stromatoporoid from Scotland. *Geol. Mag.*, 115: 53-56.
- , 1978. — History of the Ordovician continental platform and shelf margin of Australia. *J. geol. Soc. Aust.*, 25: 41-63.
- , in press a. — Ordovician stromatoporoids from the Mjøsa district, Norway. *Norsk geol. Tidsskr.*
- , in press b. — The oldest Ordovician stromatoporoids from Australia. *Alcheringa*, 3.
- , and BANKS, M. R., 1976. — *Clathrodactyon* and *Ecclimadictyon* (Stromatoporoidea) from the Ordovician of Tasmania. *Pap. Proc. R. Soc. Tasm.*, 110: 129-137.
- , and MORRIS, D. G., 1976. — New stromatoporoids from the Ordovician of New South Wales. *J. Proc. R. Soc. N.S.W.*, 109: 125-135.
- WENDT, J., 1975. — Aragonitische Stromatoporen aus der alpinen Obertrias. *N. Jb. Geol. Paläont. Abh.*, 150, 1: 111-125.
- WHITTINGTON, H. B., and WILLIAMS, A., 1964. — The Ordovician period. In Harland, W. G., Gilbert Smith, A. & Wilcock, B. (eds). *The Phanerozoic Time-scale. Quart. Jl. geol. Soc. Lond.*, 120 S: 241-254.
- WILLIAMS, A., 1962. — The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, South-West Ayrshire, with descriptions of the Brachiopoda. *Mem. Geol. Soc. Lond.*, 3: 5-267.

- , STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D., and WHITTINGTON, H. B., 1972. — A correlation of Ordovician rocks in the British Isles. *Spec. Pap. geol. Soc. Lond.*, 3: 1-74.
- WORKUM, R. H., BOLTON, T. E., and BARNES, C. R., 1976. — Ordovician geology of Akpatok Island, Ungava Bay, District of Franklin. *Can. J. Earth Sci.*, 13: 157-178.
- YABE, H., and SUGIYAMA, T., 1930. — On some Ordovician stromatoporoids from South Manchuria, North China and Chosen (Corea), with notes on two new European forms. *Sci. Repts. Tōhoku Imp. Univ.*, ser. 2, (Geol.), 14 (1): 47-62.
- YANG, K. C., and DONG, D. Y., 1962. — *Stromatoporoidea of China*: 1-40. Science Press, Peking (in Chinese).
- YAVORSKY, V. I., 1932. — Ein Stromatoporenfund im Kambrium. *Zentralbl. Min. Geol. Paläont.*, B: 613-616.
- , 1940. — Klass Hydrozoa, poryadok Stromatopory. In: *Atlas rukovodyashchikh form iskopaemykh faun S.S.S.R. Tom 1. Kembrii. Vses. nauchno-issledovat. Inst. (VSEGEI)*: 100-103.
- , 1947. — Nekotorye paleozoiskie i mezozoiskie Hydrozoa, Tabulata i Algae. *Monogr. po paleontologii S.S.S.R.*, 20 (1): 1-30. VSEGEI, Leningrad-Moskva.
- , 1955. — Stromatoporoidea Sovetskogo Soyuza, Pt 1. *Trudy ves. nauchno-issled. Geol. Inst.*, n.s., 8: 1-173.
- , 1957. — Stromatoporoidea Sovetskogo Soyuza, Pt 2. *Trudy ves. nauchno-issled. Geol. Inst.*, n.s., 18: 1-167.
- , 1961. — Stromatoporoidea Sovetskogo Soyuza, Pt 3. *Trudy ves. nauchno-issled. Geol. Inst.*, n.s., 44: 1-64.
- , 1962. — Gruppa Stromatoporoidea. Stromatoporodei. In Orlov, Y. A. (ed.), *Osnovy Paleontologii*, 2: 157-167. Izdatelstvo Akad. nauk SSSR, Moskva.
- , 1963. — Stromatoporoidea. Sovetskogo Soyuza, Pt 4. *Trudy ves. nauchno-issled. Geol. Inst.*, n.s., 87: 1-160.
- ZHURAVLEVA, I. T., 1955. — Arkheotsiaty nizhnego kembriya vostochnogo sklona Kuznetskogo Alatau. *Trudy Paleont. Inst. Akad. nauk SSSR*, 56: 5-56.
- , 1960. — *Arkheotsiaty sibirskoy platformy*: 1-344. Akad. nauk SSSR, Moskva.
- , 1970. — Porifera, Sphinctozoa, Archaeocyathi — their connections. In Fry, W. G. (ed.). *The Biology of the Porifera. Symp. zool. Soc. Lond.*, 25: 41-59.
- , and MIAGKOVA, E. I., 1974. — Stavnitelenaya kharakteristika Archaeata i Stromatoporoidea. In Sokolov, B. S. (ed.). *Drevniye Cnidaria*, 1: 63-70. Nauka, Novosibirsk.